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Association and Feeding Relationships Between *Eogammarus confervicolus* (Amphipoda, Gammaridae) and Benthic Algae on Sturgeon and Roberts Banks, Fraser River Estuary

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POMEROY, W. M., AND C. D. LEVINGS. 1980. Association and feeding relationships between *Eogammarus confervicolus* (Amphipoda, Gammaridae) and benthic algae on Sturgeon and Roberts banks, Fraser River Estuary. Can. J. Fish. Aquat. Sci. 37: 1–10.

Field and laboratory studies of the feeding and association of the gammarid amphipod *Eogammarus confervicolus* with algae and vascular plant debris were conducted on jetties, marshes, and sandflats at the Fraser River Estuary. Associations with *Prasiola meridioncalis* (alga), and debris from *Carex lyngbyei* (vascular plant) were statistically significant. Vascular plant debris was more widespread in winter (January) compared to a summer survey (August). Laboratory growth rates and survival varied with food types, which were ranked (best to worst) as follows: *Enteromorpha linza, Pylaiella littoralis, Porphyra* spp., *Navicula grevillei, Carex lyngbyei* debris and *Ulva lactuca*. Assimilation efficiencies, measured with gravimetric and radioisotope techniques (^{14}C) ranged from about 78% with *P. littoralis* to 62% with *U. lactuca*. Construction of jetties could increase the surface area for algal growth, but there would be no appreciable enhancement of primary production compared to a natural marsh/sandflat ecosystem.

Key words: Crustacea, *Eogammarus confervicolus*, benthic algae, Fraser Estuary, intertidal distribution, feeding, ecological associations, engineering structures

POMEROY, W. M., AND C. D. LEVINGS. 1980. Association and feeding relationships between *Eogammarus confervicolus* (Amphipoda, Gammaridae) and benthic algae on Sturgeon and Roberts banks, Fraser River Estuary. Can. J. Fish. Aquat. Sci. 37: 1–10.

Des études sur le terrain et en laboratoire de l'alimentation de l'amphipode gammaride *Eogammarus confervicolus* et de son association avec algues et débris de plantes vasculaires ont été effectuées sur les jetées et bancs de sable, et dans les marais de l'estuaire du fleuve Fraser. Il y a associations significatives à l'analyse statistique avec *Prasiola meridionalis* (algue) et débris de *Carex lyngbyei* (plante vasculaire). Un relevé des débris de plantes vasculaires indique que ces derniers sont plus répandus en hiver (janvier) qu'en été (août). Les taux de croissance et de survie en laboratoire varient selon les types d'aliments, dans l'ordre suivant (du mieux au pire) : *Enteromorpha linza, Pylaiella littoralis, Porphyra* spp., *Navicula grevillei*, débris de *Carex lyngbyei* et *Ulva lactuca*. L'efficacité d'assimilation, déterminée à l'aide de méthodes gravi-

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métriques et de radioisotope (^{14}C), varie d'environ 78 % chez *P. littoralis* à 62 % chez *U. lactuca*. La surface offerte à la croissance algale pourrait être augmentée par construction de jetées, mais ceci n'entraînerait pas d'augmentation appréciable de production primaire comparativement à un écosystème naturel marais/banc de sable.

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THIS study was directed toward the distribution and association of benthic algae and invertebrates on jetties and adjacent sandflats of Roberts and Sturgeon Bank at the Fraser River Estuary in southwestern British Columbia. The jetties are built with wood piling or irregularly shaped stones ("rip-rap") which supplement natural sandflat and marsh areas available for algae and invertebrates. Although communities important for fish food on "industrial substrates" (docks, breakwaters, jetties) have been documented in the coastal waters of California (Dewers and Gotshall 1974) and the North Atlantic (Nixon et al. 1973), there are no studies from the northeast Pacific. Such investigations are of special interest at present because of proposals to build new structures at the Fraser Estuary, thereby replacing or supplementing naturally occurring substrates.

The effect of such substrate changes in terms of benthic algae and use by invertebrates as cover at low tide was investigated in field studies. To determine a food link of algae with invertebrates important in fish diets, we conducted laboratory experiments using the estuarine amphipod *Eogammarus confervicolus* (Stimpson).[1] This species is used by juvenile salmonids at the Fraser (Dunford 1975), Squamish (Levy and Levings 1978), Campbell (Goodman and Vroom 1974), and Columbia River (Durkin et al. 1977) estuaries, and is one of the most ubiquitous gammarids in estuaries of the northeast Pacific. Previous studies, mostly of a preliminary nature, showed that this amphipod fed on algae (Levings 1973) and was differentially associated with certain algal species (Pomeroy 1977).

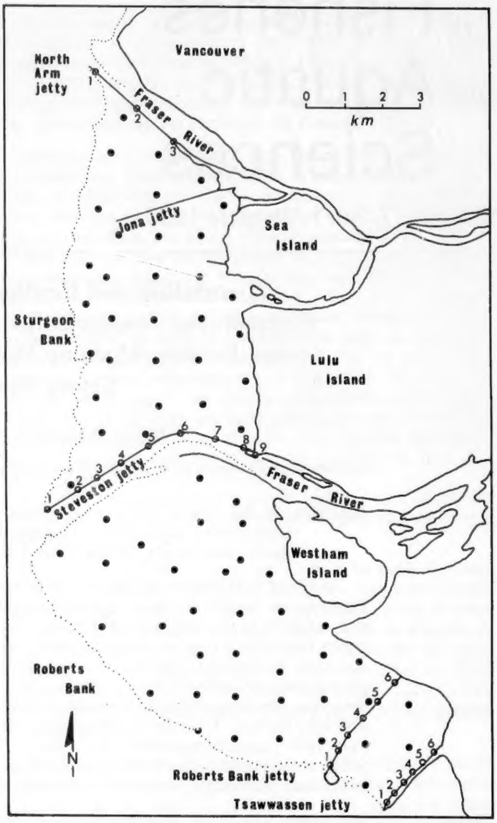

FIG. 1. Study area at the Fraser River Estuary, showing station locations on jetties and intertidal sandflats. Dotted line indicates extent of exposure at low tide.

Materials and Methods

FIELD SAMPLING FOR ASSOCIATION OF INVERTEBRATES AND COVER AT LOW TIDE

Stations were established on the four main jetties of the Fraser River Estuary, two of which are directly influenced by the river (Fig. 1). Qualitative samples of different species of algal cover material and associated invertebrates were taken at low tide from rock, wood, or sediment surfaces on both north and south sides of the jetty at each station. Sampling was done each month over the period February to June and September to December 1977.

A basket trap method (Levings 1976), was used to collect drift organisms at high tide. Traps in the form of nylon net bags 10 × 10 cm (0.5-cm mesh) were filled with a single species of algae commonly found growing on the jetties or with partially decomposed sedge (*Carex lyngbyei*) collected from adjacent intertidal marshes. All material was washed clean of organisms. The traps were placed at about 2.4 m above chart datum on rock or wood surfaces on both sides of the North Arm Jetty at Stations 1, 2, and 3 (Fig. 1) for a period January 31 to February 13, 1978. In a subsequent experiment, larger traps (12 × 20 cm; 1.2-cm mesh) were placed at Station 3 on pilings (about 2.4-m level) isolated from the jetty by sandflats about 30-m wide. These traps were exposed from March 3 to 28, 1978. All traps were recovered at low tide to collect invertebrates seeking cover on the ebb tide. The positioning of several traps at the same station, each containing a different material, tested for choice of cover type.

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[1] Until Bousfield's recent publication (1979), this species was referred to *Anisogammarus confervicolus*.

The intertidal sandflats of Roberts and Sturgeon Bank were also sampled for invertebrate/cover association. Qualitative samples were taken at low tide during January 8–10, 1978 and August 16–18, 1978 from stations indicated on Fig. 1. Some stations could not be sampled due to unfavourable tide level or inaccessibility to the Canadian Coast Guard Hovercraft used for sampling the extensive intertidal flats.

LABORATORY EXPERIMENTS WITH *Eogammarus confervicolus*

To facilitate measurements of weight changes during growth, we derived a relationship between head length (mm) and body weight (mg dry wt) initially for a combination of 50 field and laboratory cultured individuals. Amphipods were measured and then dried to constant weight at 100°C. The amphipods were ashed in a muffle furnace at 500°C for 4 h to arrive at ash-free dry weight. Using these data, the relationship between dry weight and ash-free weight was determined.

Growth experiments were conducted using as food sources the dominant benthic algae found on the jetties (*Navicula* sp. — colonial diatom, *Pylaiella littoralis*, *Porphyra* spp., *Ulva lactuca*, *Enteromorpha linza*) and partially decayed sedge (*Carex lyngbyei*). Growth was determined at salinities of 5, 15, and 20‰, and temperatures of 4 and 10°C.

Juvenile amphipods collected from ovigerous females obtained on Sturgeon Bank (October 1977) were acclimated to appropriate combinations of salinity and temperature for 2 wk prior to use in experiments. During this period they were fed on a mixture of food sources to be used in the forthcoming experiments.

Experimental growth chambers consisted of covered plexiglass compartmentalized boxes (5 × 5 × 5 cm), each compartment containing 80 mL of filtered water (0.45 μm). A measured amphipod was placed in each compartment with an excess of food. Several replicates were set up for each food/salinity combination, the number being dependent upon the availability of juvenile amphipods. Duplicate chambers were prepared for the various food sources and salinities, one set in a culture chamber at 10°C and one in a cold room at 4°C, both with a photoperiod of 12 h. Head length measurements were made at weekly intervals with the animals being replaced in clean filtered water and supplied with fresh excess food. Animals were immobilized in moist cotton batting while measurements were made with a stereomicroscope. Growth and survival rates were followed for a period of 12 wk or until death of all the amphipods, which ever occurred first.

Six replicates of the different food sources were dried to constant weight at 80°C (Paine 1971). The samples were then ground to a fine powder, subsamples taken and burned in a Phillipson Microbomb Calorimeter to determine kilo Joules per gram ash-free dry weight.

Assimilation efficiencies were determined for adult and juvenile amphipods using food sources previously noted. Amphipods were first acclimated to 10°C and 15‰ salinity for 2 wk. Two techniques were then used for comparative purposes with the same amphipods and food used in both. A dry wt: ash-free dry wt method was tried first.

Conover (1966) derived a formula to calculate assimilation efficiency (A) based on the assumption that absorption of the inorganic component of the food is negligible. To obtain estimates of efficiency using this method, we placed an amphipod in a feeding chamber at 15‰ salinity, with excess food in a culture chamber at 10°C for 16 h. Ten replicates were done for each food source. A nitex screen (500 μm) and plexiglass stand prevented re-ingestion of fecal pellets which fell to the bottom. Following the feeding period, pellets were collected and filtered onto a pre-ashed and weighed GF/C filter. A small amount of each food source was also placed on a GF/C filter. Dry weights and ash-free dry weights were determined and values inserted in the formula

$$A = \frac{(F - E)}{(1 - E)F} \times 100$$

where: F is the ratio of ash-free dry wt: dry wt in the food and E a similar ratio for the feces. This method has the advantage of not requiring the quantitative collection of fecal pellets.

TABLE 1. Common species of macroalgae recorded from the jetties and sandflats of Sturgeon and Roberts banks and which are potentially useful as cover for invertebrates.

Algae	Comments
Chlorophyta	
Enteromorpha linza	north and south side all jetties, mid-upper intertidal, winter and spring.
Ulva lactuca	south side North Arm jetty, North side other jetties, upper intertidal, winter and spring.
Monostroma fuscum	south side North Arm jetty, North side Steveston jetty, upper intertidal, winter and summer.
Prasiola meridionalis	north and south side of all jetties; upper intertidal winter and spring.
Rhizoclonium riparium	as drift and in tide pools or sandflats; upper intertidal in summer.
Lola lubrica	as drift on sandflats; spring.
Phaeophyta	
Fucus distichus subsp. *edentatus*	on all jetties, Steveston jetty — north side only; low intertidal in winter.
Pylaiella littoralis	north side of Steveston jetty; low to mid intertidal in winter.
Porphyra perforata *Porphyra sanjuanensis*	north and south sides of North Arm and Steveston jetties; low to high intertidal in winter.
Laminaria sp.	as drift on sandflats; lower intertidal in winter.
Chrysophyta	
Melosira moniliformis *Navicula grevillei*	tidal depressions on sandflats, mid to upper intertidal in winter.

TABLE 2. χ^2 analysis of association of *Gnorimosphaeroma oregonensis* (left panel) and *Eogammarus confervicolus* (right panel) with cover types. N = north side; S = south side of jetty; * indicates association significant at $P = 0.05$; NS = not significant, $P > 0.05$.

	Gnorimosphaeroma oregonensis																*Eogammarus confervicolus*[a]			
	North Arm jetty				Steveston jetty				Roberts Bank				Tsawwassen				Steveston jetty			
	Winter		Spring		Winter		Spring		Winter		Spring		Winter		Spring		Winter		Spring	
Algal species	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S
Enteromorpha linza	+[b]	NS	−[b]	+	NS	+	*	−	+	−	+	+	NS	NS	NS	NS	NS	NS	NS	+
Ulva lactuca	−	NS	−	+	+	−	NS	−	+	−	+	−	NS	−	NS	−	+	+	NS	−
Monostroma fuscum	−	−	−	+	NS	+	NS	+	−	−	−	−	−	−	NS	−	NS	NS	NS	+
Prasiola meridionalis	+	*	−	+	NS	+	NS	−	+	+	+	+	+	+	+	+	*	NS	NS	−
Fucus distichus	+	NS	+	+	NS	−	NS	−	+	+	+	+	+	NS	−	NS	NS	+	NS	−
Porphyra spp.	+	NS	+	−	NS	+	−	−	+	−	−	−	+	−	−	−	NS	+	−	−

[a]Absent on other jetties.

[b]+ indicates algae present, invertebrates absent; − indicates algae absent.

The second method of determining assimilation efficiency was based on ^{14}C uptake and incorporation as described by Chang (1975). Briefly, benthic algae were rinsed several times in filtered seawater (0.45 μm) and placed in 500 mL flasks with 250 mL filtered seawater (15‰ salinity). Each flask was labelled with 20 μCi $NaH^{14}CO_3$ (1 Ci = 37 GBq) and placed in an incubation chamber for 1 wk at 10°C and a photoperiod of 12 h. At the end of this period, the algae were rinsed several times in filtered seawater to remove external ^{14}C before use in the feeding experiment. A measured amphipod was rinsed with filtered seawater, placed in a 125 mL flask with 100 mL filtered seawater and excess labelled food. Flasks were sealed and incubated in the dark at 10°C for 16 h. Control flasks were set up with labelled algae but without an amphipod to determine background exudation rates of the algae. At the end of 16 h, each amphipod was transferred to a flask with filtered seawater and excess unlabelled algae, for another 8 h to clean the gut of labelled food. The amounts of ^{14}C in solution in both feeding flasks, in feces, and in the amphipods were measured by counting on a Packard Tri-Carb Liquid Scintillation Spectrophotometer (Model 3375).

Results

ASSOCIATION OF INVERTEBRATES SPECIES AND COVER TYPE

The benthic algae recorded from the rock jetty surveys are given in Table 1. The algae listed are those present in sufficient abundance to be potentially useful as sites of invertebrate concealment at low tide. Of these, the most widely distributed was *E. linza*, being found throughout the intertidal on all jetties; *U. lactuca*, *M. fuscum*, and *F. distichus* were also recorded from all areas but with more restricted distribution in the intertidal. *Porphyra* spp. and *Prasiola meridionalis* were found in great abundance, mainly on the Steveston and North Arm jetties. Algal communities on the latter structure were similar on both sides of the jetty. Other jetties showed north–south variation with respect to algal growth. Most of the algal growth on the Steveston and Roberts Bank jetties occurred on the north sides, while on the Tsawwassen jetty most algal growth was on the south side.

Two species of invertebrates, the amphipod *E. confervicolus* and the isopod *Gnorimosphaeroma oregonensis*, were selected for detailed analysis regarding their association with benthic algae. *Eogammarus confervicolus* was found associated with attached macroalgae only on the Steveston jetty (Table 2) but the only significant association ($P < 0.05$) was with *P. meridionalis* on the north side of the jetty in winter. In comparison, *G. oregonensis* had considerably higher association with macroalgae on all jetties except Roberts Bank (Table 2). As with *E. confervicolus*, most of the associations were not found to be significant with the exception of *P. meridionalis* on the North Arm and *E. linza* on the Steveston jetty. Both of these associations occurred on the delta side of the dykes, away from the effect of direct river flow.

Invertebrates were recorded from 12 of the 24 basket traps placed in contact with rip-rap of the North Arm jetty at Stations NJ1-3. *Fucus distichus* and decaying sedge collected the majority of the invertebrates, with higher concentrations on the north side of the jetty at NJ3. The only amphipod recorded was *Hyale plumulosa* which was also very abundant under rocks on the jetty. Overall, *G. oregonensis* was the dominant invertebrate recovered, being associated with all cover types.

Basket traps placed on pilings about 30 m from the North Arm jetty, over sandflats (south side), were virtually devoid of invertebrates after being exposed for 28 d. *Carex lyngbyei* and *U. lactuca* on the south side of the jetty collected only one chironomid larva and one *G. oregonesis*.

The distribution pattern for cover material (algae, wood, etc.) and invertebrates on the intertidal flats from a midwinter sampling is presented in Fig. 2.

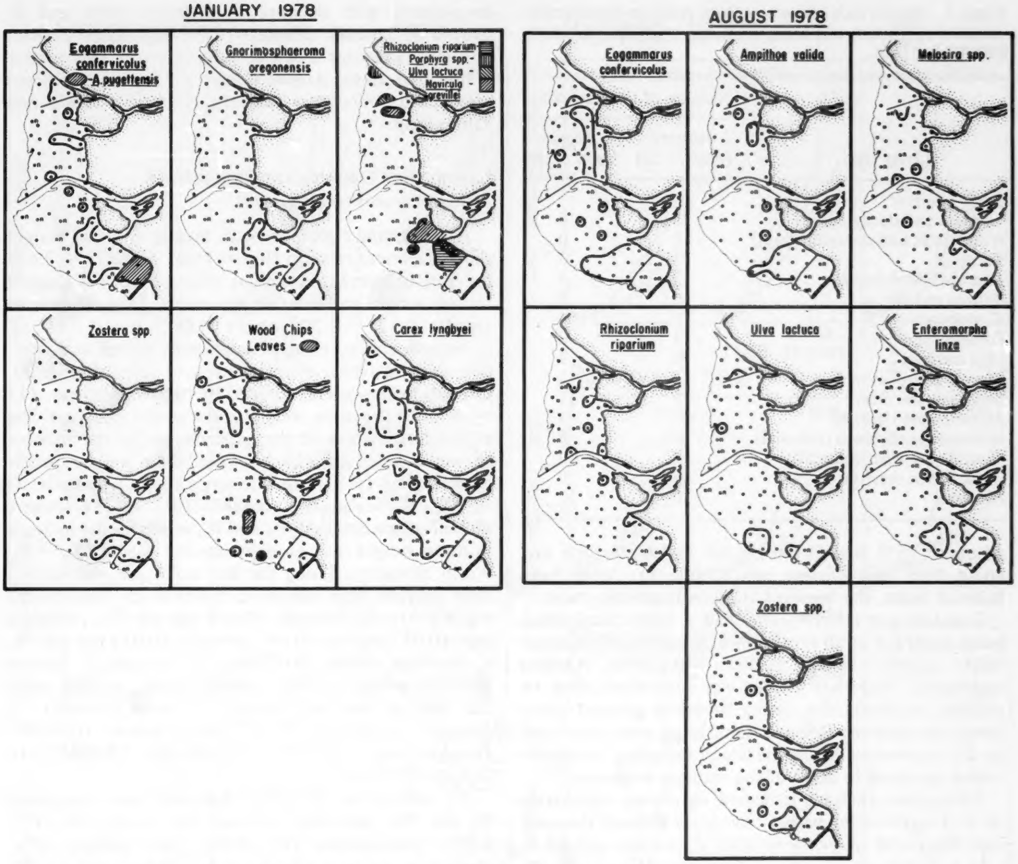
JANUARY 1978
Eogammarus confervicolus
A. pugettensis
Gnorimosphaeroma oregonensis
Rhizoclonium riparium
Porphyra spp.
Ulva lactuca
Navicula grevillei
Zostera spp.
Wood Chips
Leaves
Carex lyngbyei
AUGUST 1978
Eogammarus confervicolus
Ampithoe valida
Melosira spp.
Rhizoclonium riparium
Ulva lactuca
Enteromorpha linza
Zostera spp.

FIG. 2. Distribution of organisms (enclosed in heavy lines) and cover types on Sturgeon and Roberts banks in January 1978 (left panel) and August 1978 (right panel). *n* indicates station not sampled.

Localization of some cover types is evident with *Zostera marina* restricted to southern Roberts Bank around Roberts Bank causeway and between it and Tsawwassen causeway. *Porphyra* spp., *E. linza*, and *M. fuscum* were recorded near jetties on which they were found growing. *Carex lyngbyei*, intact and decaying, was well distributed over the intertidal flats, being more common in the mid and upper regions, seaward of marsh areas described by other authors (e.g. Yamanaka 1975). Of the 52 stations sampled *C. lyngbyei* occurred in 48%, wood in 19%, roots in 14%, and *Z. marina* in 12% (Table 3). Only 19% of the stations sampled had no cover of any type, and these were located primarily on the seaward portion of the intertidal flats (Fig. 2).

Although several species of invertebrates were recovered from the collected cover material, only amphipods and isopods are considered in detail. Of the stations sampled, *G. oregonensis* was recorded primarily on southern Roberts Bank (Fig. 2). *Anisogammarus pugettensis*, not recorded on the jetties, occurred mainly between Roberts Bank and Tsawwassen jetties; *E. confervicolus* was found on both Roberts and Sturgeon Banks in mid and upper intertidal regions; *G. oregonensis* occurred in 29% of the stations sampled, *A. pugettensis* in 8% and *A. confervicolus* in 45%.

Conditions of cover and invertebrate distribution for late summer (August) varied considerably compared to midwinter (Fig. 2). *Carex lyngbyei* debris was absent, with macroalgae taking its place. Localization was evident with *R. riparium* being found primarily on Sturgeon Bank and *U. lactuca*, *E. linza*, and *Zostera* spp. primarily on southern Roberts Bank throughout the intertidal. Of the 58 stations sampled, 52% had

TABLE 3. Occurrence of various cover types on the intertidal sandflats of Roberts and Sturgeon banks recorded in January and August 1978.

Cover type	Number of times recorded January (max. = 52)	 August (max. = 58)
Carex lyngbyei (intact and decaying)	25	0
Wood (drift and decaying chips)	10	0
Roots	7	0
Tree and shrub leaves	3	0
Zostera marina	6	2
Z. americana	0	4
Porphyra spp.	1	0
Ulva lactuca	0	8
Monostroma fuscum	1	0
Enteromorpha linza	1	11
Rhizoclonium riparium	0	9
Melosira moniliformis (colonial)	0	8
Navicula grevillei (colonial)	2	0
Unidentified material	6	0
No cover	10	31

no cover, 18% had *E. linza*, 13% had *U. lactuca*, and about 10% had *Zostera* spp. (Table 3). Aside from Roberts Bank, the seaward stations had little cover.

Eogammarus confervicolus had a wide distribution, being recorded at all levels from Roberts and Sturgeon banks in 40% of the stations with cover. Another amphipod, *Ampithoe valida*, was somewhat more restricted in distribution, being found in greatest abundance on southern Roberts Bank in an area dominated by *G. oregonensis* during the winter sampling. *Ampithoe valida* occurred in 26% of the stations with cover.

Chi-square analyses indicated significant association of *E. confervicolus* with *C. lyngbyei* (intact, decayed, and roots), *A. pugettensis* with *Z. marina* and of *G. oregonensis* with decayed *C. lyngbyei* roots and *Z. marina* in January (Table 4). No significant association was noted for wood or general particulate matter at this time. In the August sampling, the only significant association found was between *Ampithoe valida* and *Zostera* spp.

LABORATORY GROWTH AND SURVIVAL OF *Eogammarus confervicolus*

A logarithmic plot of head length and dry weight showed a linear relation (log wt (mg) = 0.213 + 3.478 log length (mm)). A similar relationship was evident for dry weight and ash-free dry weight (log ash-free wt (mg) = 0.121 + 1.209 log dry wt (mg)).

Growth and survival of amphipods varied as a function of food types, temperature, and salinity (Fig. 3). Growth rates were determined by two calculations: (1) by dividing the mean weight of the amphipods surviving at the termination of the experiments by the number of weeks involved (2) by calculating weight-specific growth rates (G) using Winberg's (1971) formula: $G = \log_{10} W_2 - \log_{10} W_1 / (0.4343 \quad (T_2 - T_1))$, where the difference between W_2 and W_1 indicates the increase in mean weight over an experimental period ($T_2 - T_1$; 7 d in all cases). Using the first technique, the various food sources were ranked as follows: *E. linza* (0.103 $\text{mg} \cdot \text{wk}^{-1}$); *P. littoralis* (0.058 $\text{mg} \cdot \text{wk}^{-1}$); *Porphyra* spp. (0.057 $\text{mg} \cdot \text{wk}^{-1}$); *N. grevillei* (0.034 $\text{mg} \cdot \text{wk}^{-1}$); *C. lyngbyei* debris (0.039 $\text{mg} \cdot \text{wk}^{-1}$); and *U. lactuca* (0.026 $\text{mg} \cdot \text{wk}^{-1}$). With weight-specific growth rates, the ranking was very similar; *E. linza* (0.0485); *P. littoralis* (0.0434); *C. lyngbyei* debris (0.0345); *Porphyra* spp. (0.0339); *N. grevillei* (0.0336); *U. lactuca* (0.0334).

An analysis of variance on growth rates calculated by the first technique showed that food type ($P < 0.05$), temperature ($P < 0.05$), and salinity ($P <$

TABLE 4. χ^2 analysis showing relationships of invertebrates and cover type on the intertidal sandflats on Sturgeon and Roberts banks. Upper panel: January 1978. Lower panel: August 1978. * indicates association significant at $P = 0.05$.

Cover type	*Eogammarus confervicolus*	*Anisogammarus pugettensis*	*Gnorimosphaeroma oregonensis*
Carex lyngbyei (sedge)			
intact	*	NS	NS
decayed	*	NS	*
roots	*	NS	*
Zostera marina (eelgrass)	NS	*	*
Unidentified particulate matter	NS	NS	NS

Cover type	*Eogammarus confervicolus*	*Ampithoe valida*
Zostera spp.	NS	*
Rhizoclonium riparium	NS	NS
Enteromorpha linza	NS	NS
Ulva lactuca	NS	NS

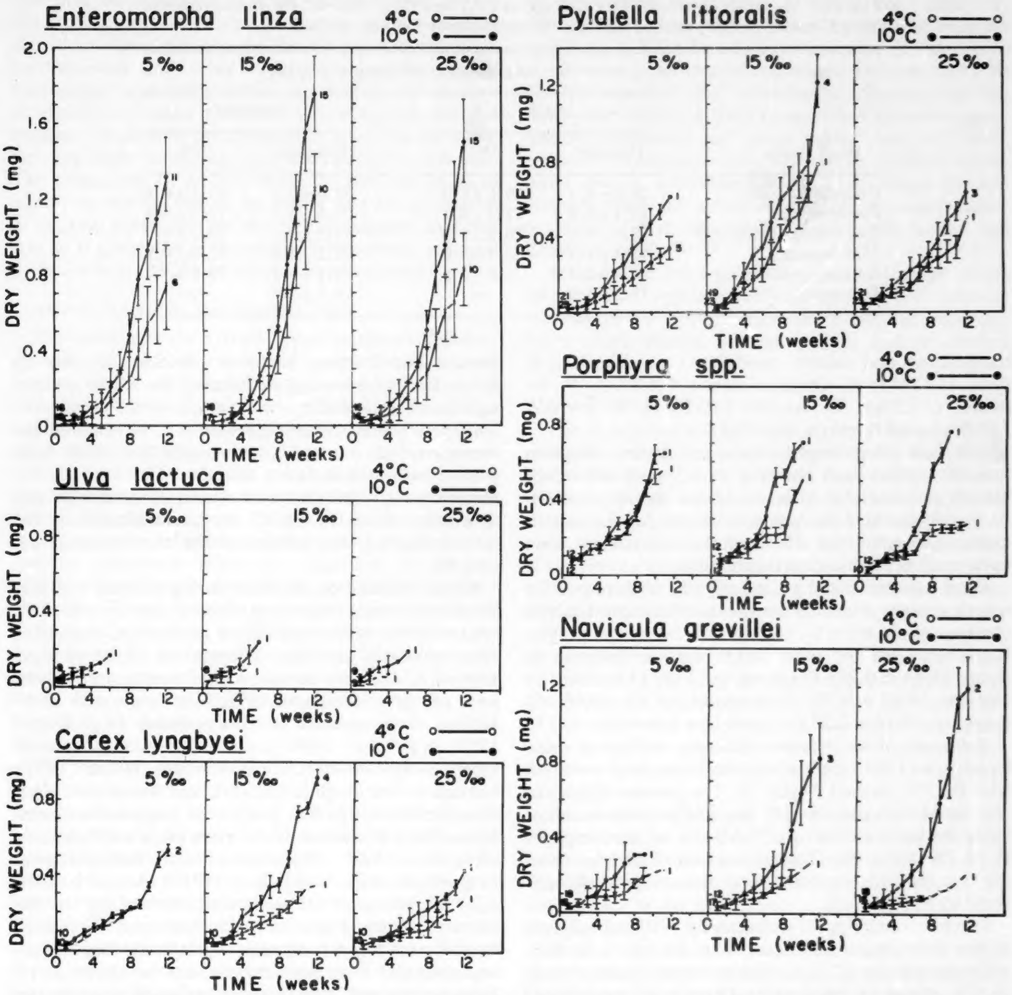

FIG. 3. Growth in weight and survival of *Eogammarus confervicolus* cultured on six food types. Numbers at the origin of graphs indicate amphipods at beginning of experiments, and those at end of growth plots show number surviving.

0.05) independently influenced amphipod growth at our experimental conditions, but weight-specific growth rates were affected only by food type ($P < 0.05$) and temperature ($P < 0.05$).

Survival data are presented in Fig. 3. Numerals near the origin of growth lines indicate numbers at the beginning of an experiment and those near the ends show number alive at its termination. Mortality ended the experiments with *U. lactuca* after 4–6 wk, but animals fed on the other species survived for 10–12 wk, when the study ended. At 6 wk, survival on the various food sources (averaged over temperature and salinity conditions) was as follows: *E. linza* (87.6%), *C. lyngbyei* debris (73.3%), *P. littoralis* (67.7%), *Porphyra* spp. (64.5%), *N. grevillei* (43.1%), and *U. lactuca* (5.8%). An analysis of variance with data from the six experimental conditions (after arc–sine transformation) showed that food type ($P < 0.05$) and salinity ($P < 0.05$) influenced survival. Six weeks later, when the experiments ended, amphipods fed on all the food sources except *E. linza* had suffered substantial mortality but the ranked order (survival averaged over

TABLE 5. Assimilation efficiencies (% ± SD) at 15‰ and 10°C obtained for *E. confervicolus* using Conover's (1966) method and the ^{14}C uptake-incorporation method.

	Assimilation efficiency (% ± SD)			
	Adult		Juvenile	
Food source	Conover	^{14}C	Conover	^{14}C
Pylaiella littoralis	78.2±4.1	79.6±6.0	78.6±6.3	83.5±8.8
Porphyra spp.	70.8±5.4	73.2±6.1	76.6±3.9	77.3±6.4
Enteromorpha linza	71.6±4.0	76.2±5.0	74.3±4.5	77.2±5.9
Ulva lactuca	62.4±5.9	62.1±8.6	71.1±8.6	67.8±4.9
Navicula grevillei	55.7±5.4	76.6±6.9	60.1±6.5	79.9±5.7
Carex lyngbyei	71.0±5.1	—	76.3±5.7	—

temperature and salinity conditions) was similar: *E. linza* (66.3%), *C. lyngbyei* debris (16.7%), *P. littoralis* (13.2%), *U. lactuca* (12.2%), *N. grevillei* (10.2%), and *Porphyra* spp. (8.3%).

Although interactions between salinity and temperature have often been observed to influence laboratory growth and mortality of invertebrates, the above statistical analyses show this was not the case for our experiments. The combined effects of these conditions were apparently not influencing these results.

Food sources tested varied slightly with respect to caloric content. *Navicula grevillei* had the highest caloric content at 21.64 ± 0.21 kJ/g ash-free dry weight. Equivalents for the other foods were as follows: *E. linza*: 20.34 ± 0.29; *Porphyra* spp.: 20.13 ± 0.38; *U. lactuca*: 19.92 ± 0.25; *P. littoralis*: 19.17 ± 0.38; *C. lyngbyei*: 19.12 ± 0.29 kJ/g ash-free dry weight.

Estimates of assimilation efficiency arrived at using Conover's (1966) method are similar to those obtained with the ^{14}C method (Table 5). The greatest difference was noted with diatoms (*N. grevillei*) where estimates using the latter method are 76.6% for adults compared to 55.7% from the Conover method. Estimates from the two methods on other food sources generally differed by less than 5%.

Juvenile amphipods consistently showed slightly higher assimilation efficiences than did adults in both methods and for all food sources tested (Table 5), up to 9% greater in some cases. Overall, *P. littoralis*, *E. linza*, and debris from *C. lyngbyei* has the highest assimilation efficiencies and *N. grevillei* the lowest.

Discussion

DISTRIBUTION AND COVER ASSOCIATION

Distribution of the amphipod *Eogammarus confervicolus* and its cover association with attached algae on rock jetties of the Fraser Estuary is limited. Its occurrence on the delta side of the Steveston jetty in association with light growths of *P. meridionalis* is in an area adjacent to a sedge marsh which has high numbers of *E. confervicolus* (W. M. Pomeroy unpublished data). In contrast to the jetties, wide distribution and cover association occur on the intertidal sandflats of both Roberts and Sturgeon banks. A selection for cover by *E. confervicolus* is suggested during the winter when a significant relationship was noted with sedge (*C. lyngbyei*) debris. Certain differences in associations between invertebrates and cover material may result from passive rather than active selection. For example the nonassociation observed between *E. confervicolus* and *Z. marina* debris (Table 4) may be explained by the nonoverlapping distribution of the two potential associates.

Cover material on sandflats during summer was predominantly macroalgae and *Zostera* spp. for which *E. confervicolus* had no significant preference, suggesting acceptability of all types. Filamentous forms of algae such as *E. linza* did contain higher numbers of amphipods per gram compared to thallose forms such as *U. lactuca*. Investigations of rocky shores (e.g. Weiser 1952; Nassichuk 1975) have emphasized the cover aspect of algal–invertebrate associations. Weiser (1952) worked on the English Channel, and found that algae characterized by growth forms with large surface areas (e.g. a "tufted" species — *Gelidium corneum*) harbored more invertebrates than species with flattened thalli (e.g. *Porphyra laciniata*). Kito (1975) showed how the algae *Sargassum confusum*, characterized by an extremely branched growth form, harbored very large numbers of "phytal animals." "Artificial *Sargassum*," manufactured from polyethylene, can be almost as effective as natural algae in attracting small invertebrates (Yoshihara et al. 1977).

Morphological interactions such as these may in part explain the lack of *E. confervicolus* in algae on the jetties. The dominant algal species, *Porphyra* spp. and *U. lactuca*, were thallose and provided relatively poor protection from wave shock and desiccation. The slow growth and high mortality of *E. confervicolus* fed on *U. lactuca* and *Porphyra* spp. suggests these algae are not suitable from a nutritional viewpoint.

Other possible explanations for lack of occurrence and cover association on jetties may be either that the amphipods have a preference for marsh grass habitat where they occurred in high numbers or that they seek cover amongst the rip-rap, becoming part of the crevice community at low tide. Preliminary sampling suggests this may be occurring to some extent. Cover among the rip-rap provides better protection against desiccation than algae growing on the rip-rap. *Eogammarus confervicolus* and other invertebrates make use of macroalgae and sedge debris as cover in the absence of rip-rap or marsh plants as shown by our sandflat studies. Amphipods occurring with cover on the sandflats are likely retreating from the marshes at ebb tide. The absence of *H. plumulosa* on the flats and in algae higher on the rip-rap of the jetties and its abundance in organic debris low on the rip-rap suggests that this species is a member of the crevice community, as found by Nassichuk (1975) on nearby Bowen Island.

GROWTH, SURVIVAL, AND ASSIMILATION

The reason various food types produced different growth and survival cannot be ascertained from the present results. A number of factors may be responsible. It is possible, for example, that each algal species has characteristic microorganisms (bacteria, microalgae, and protozoans) that *E. confervicolus* utilized as a food source in addition to actual plant tissue. This has often been suggested as a main feeding mechanism for amphipods (Hargrave 1970). Palatability and ease of manipulation of algae with the mouth parts may be another important factor as suggested by Martin (1966). Best growth and lowest mortality, averaged over all salinities and temperatures, occurred with *E. linza* and *P. littoralis*, both filamentous species easily manipulated by the amphipods. These species provide ample refuge space for invertebrates, especially juvenile forms (Pomeroy 1977). Similar feeding refugia were described by Jansson (1966) for amphipods in the "*Cladophora* belt" of the Baltic Sea.

Our results show that the growth rates of *E. confervicolus* were slightly lower than those reported for *A. pugettensis* by Chang (1975). At 10°C and 24‰, *A. pugettensis* grew on *Enteromorpha intestinalis* at approximately 0.20 mg·wk^{-1}, wheras rates for *E. confervicolus* on the same genus of algae, at identical temperature and approximately the same salinity conditions (25‰), were about 0.13 mg·wk^{-1}. As the penultimate size of *A. pugettensis* is larger than that of *E. confervicolus* it is likely that the growth differences reflect a species-specific characteristic. Laboratory growth rates for *Gammarus pulex* and *G. pseudolimnaeus* fed debris from decaying leaves (elm (*Ulmus carpinifolia*), oak (*Quercus* sp.)) were considerably higher, at about 0.7 mg·wk^{-1} (Willoughby and Sutcliffe 1976).

For amphipods fed on *E. linza* there was a positive relationship between growth rates and survival to 12 wk. For other food types the relationship was more complex, but even for *E. linza* most mortality occurred in the 6–12 wk period. Similarily, Chang (1975) observed that mortality for laboratory-reared *A. pugettensis* was higher after 9 wk. In contrast, Nilsson (1977) reared *Gammarus pulex* in group cultures (>25 animals per test chamber) and found the highest mortality during the first 4 wk of the experiment.

Assimilation efficiencies (A.E.) for adult *E. confervicolus* were slightly lower than those reported by Chang (1975) for *A. pugettensis* fed *E. intestinalis* at the same experimental conditions. Dulepov and Pois (1975) reported that assimilation efficiency for the freshwater species *A. kygi* (unspecified size and experimental conditions) fed "plant debris" was 59% (^{14}C method). *Gammarus pseudolimnaeus*, another freshwater species, assimilated 40–75% of fungal mycelia but only 10% of american elm (*Ulmus americana*) or maple (*Acer saceharum*) leaves (Barlocher and Kendrick 1975).

Assimilation efficiencies on algae and sedge debris corresponded approximately to growth and survival data, as the lowest A.E. values were obtained with food types which yielded poorest, growth and/or survival (e.g. *U. lactuca*, *C. lyngbyei*).

ALGAL BIOMASS ON JETTIES

The rock jetties of the Fraser Estuary act as artificial production units, favoring the growth of macroalgae which do not normally grow on the sandflats. With a few assumptions we have calculated the surface area available for algae on the rip-rap used on training structures, specifically the Steveston jetty. The dimensions of the rip-rap armoring this structure are approximately 1.2 m on each side. Assuming the rocks are cubical and that the outer one-third of the rip-rap (i.e. the portion facing the river) might be available, each block would present about 3.39 m^2 of surface area. The width of the sloping bank of rip-rap is approximately 15 m. Therefore, for each kilometre of jetty approximately 33 920 m^2 (3.4 ha) is presented. The north side of this particular jetty is exposed to water for only about two-thirds of its length so further calculations are restricted to the river side.

Our studies determined that *E. linza* is one of the most widespread algae on the jetties. In June 1978 the biomass of *E. linza* was obtained by scraping the algae from the rock surface at 13 random locations on the sloping face of the jetty. Mean biomass was 135 g·m^{-2} dry wt, equivalent to about 54 g C·m^{-2}.

Sandflats adjacent to rock jetties have microalgae (primarily diatoms) as the major primary producers. Macroalgae such as those found on the jetties as well as eelgrass are present in isolated tidal pools, surface patches or as drift partially buried in the sand. It is in these which invertebrates seek cover on an ebb tide.

The available sandflat habitat (Sturgeon, Roberts Bank) has been estimated at 130×10^6 m^2 (about 13 000 ha) or about 98 times that available on the five rock jetties of the foreshore. Considering microalgae in the top 1 cm of substrate to be active primary producers, an average of 0.67 g C·m^{-2} (0.03–2.19 g) was present in January 1878 compared to 0.89 g C·m^{-2} (0.02–3.55 g) in August 1978 (Pomeroy and Levings unpublished data). These biomass estimates are based on active chlorophyll *a* values and thus represent only the organic carbon present in the algae making comparison with algal biomass on the jetties possible.

On a metre square basis, the organic carbon represented by diatoms on the sandflats seems small compared to that made available by macroalgae on the jetties. However, the large extent of sandflat substrate coupled with continued organic input throughout the year and a rapid turnover rate likely result in very high organic input for this substrate as noted at the Squamish estuary (Pomeroy 1977). In that study, a turnover time of 4 d was noted for a sandflat diatom association and an average of 22 d for *Enteromorpha* spp. The latter algae had an average net productivity of 0.69 g $C \cdot m^{-2} \cdot d^{-1}$ compared to 0.32 for sandflat diatoms. In terms of yearly net production per meter square, the value of *Enteromorpha* was about 20% higher than sandflat diatoms. Considered over the distribution area, net production for *Enteromorpha* amounted to only 3% of that attributed to microalgae on the sandflats. A somewhat similar situation is assumed for the Fraser Estuary.

In terms of function in the estuarine ecosystem, rock jetties provide a stable substrate for the growth of macroalgae which, along with the rip-rap provide cover and food for cerain invertebrates forming part of a "crevice" community. Macroalgae on the sandflats also act as cover and food for invertebrates, especially those being removed from the marshes at ebb tide. Microalgae on the sandflats provide an abundant, continually present source of energy, augmented by organics from the marsh and from jetty macroalgae.

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Effect of Walleye (*Stizostedion vitreum vitreum*) Predation on Juvenile Mortality and Recruitment of Yellow Perch (*Perca flavescens*) in Oneida Lake, New York[1]

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NIELSEN, L. A. 1980. Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. Can. J. Fish. Aquat. Sci. 37: 11–19.

The abundance of 12 year-classes of yellow perch (*Perca flavescens*) in Oneida Lake, New York, was estimated at intervals between ages 0 and II from catch and area swept by trawls. Rankings of abundance of year-classes changed between the ends of the first and third growing seasons, suggesting that ultimate year-class strength was influenced strongly by mortality of age I and II fish. Predation by walleyes was probably the principal cause of mortality of age I and II perch. Although frequency of occurrence of age I and II perch in stomachs of walleyes was low, several lines of evidence suggested that density of juvenile perch also was low and that walleyes consumed a large proportion of each perch cohort. Rates of mortality were modified by perch length, perch density, and density of age 0 perch, all of which relate to intensity of walleye predation.

Key words: yellow perch, walleye; mortality, predation; Oneida Lake

NIELSEN, L. A. 1980. Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. Can. J. Fish. Aquat. Sci. 37: 11–19.

L'abondance de 12 classes d'âge, entre les âges 0 et II, de perchaudes (*Perca flavescens*) du lac Oneida, New York, a été estimée à intervalles à même les prises et dans la région balayée par les chaluts. Les rangs d'abondance changent entre la fin de la première saison de croissance et la fin de la troisième, ce qui donne à penser que l'abondance ultime des classes d'âge est fortement influencée par la mortalité des poissons d'âge I et II. La principale cause de mortalité des perchaudes d'âge I et II est probablement la prédation par le doré jaune. Bien que les perchaudes d'âge I et II ne fussent pas trop communes dans les estomacs de dorés, on a plusieurs indices à l'effet que la densité des jeunes perchaudes était faible et que les dorés jaunes avalaient une forte proportion de chaque cohorte de perchaudes. La longueur et la densité des perchaudes, ainsi que la densité des perchaudes d'âge 0, toutes liées à l'intensité de la prédation par les dorés, affectent le taux de mortalité.

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MECHANISMS regulating abundance of yellow perch (*Perca flavescens*) have attracted attention because variable year-class abundance is common to most percid populations (Koonce et al. 1977). The premise that cohort strength is set during a critical period early in life has led to studies in which indices of adult abundance are related to factors affecting egg and larval mortality rates. Temperature, wind conditions, turbidity, water level, food availability, and predation have probable impacts on year-class strength, but attempts to generalize population models have met with limited success.

Variable mortality may continue beyond early phases of the life cycle and influence cohort abundance over an extended period. Whereas environmental factors within normal ranges are unlikely to cause mortality of juvenile fish, predation may continue at high rates if prey remain vulnerable to predators. Forney (1976) suggested that cannibalism late in the first year of life was a primary determinant of the abundance of age IV walleyes in Oneida Lake. Cohorts of yellow perch in Oneida Lake varied 45-fold in relative abundance at age 0 (Forney 1971), but 300-fold by age III (Clady 1976). Since information regarding the dynamics of juvenile perch is virtually nonexistent, the importance of the juvenile period is difficult to assess. This study was designed to evaluate the effect of walleye predation on the mortality and recruitment of yellow perch in

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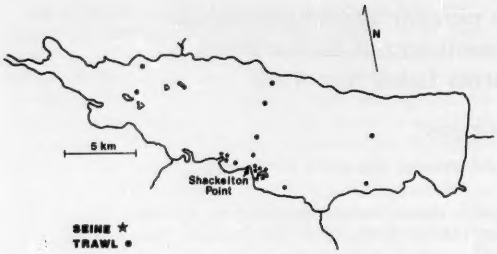

FIG. 1. Oneida Lake, showing locations of sampling sites.

Oneida Lake between age 0 in October and age II.

Oneida Lake, a glacial lake located in central New York, has been the site of extensive limnological and fisheries research, summarized by Mills et al. (1978). The lake covers 206.7 km^2 and has a maximum depth of 16.8 m and mean depth of 6.8 m. Within a diverse fish fauna of more than 50 fish species, yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*) are most abundant. Age 0 yellow perch comprise more than 80% of the catch of small fish in benthic trawls during most years (Forney 1971), and adult walleyes and yellow perch were 22 and 64%, respectively, of gillnet catches during 1962–1973 (Clady 1974). Although Oneida Lake is known primarily for walleye fishing, anglers catch similar numbers of yellow perch and walleyes (Grosslein 1961). The primary food chain producing these sport fishes is via zooplankton eaten by larval and fingerling walleyes and by yellow perch of all ages. Age 0 yellow perch are the principal food of juvenile and adult walleyes.

Materials and Methods

ESTIMATES OF YELLOW PERCH ABUNDANCE

Abundance of age 0, I, and II yellow perch (hereafter also written as perch) was estimated from the catch in a benthic trawl during 1962–74. The trawl, which had a 5.9-m footrope, 30-mm stretch mesh in the body, and 13-mm stretch mesh in the cod end, was hauled during daylight at 8–10 sites where water was deeper than 4 m (Fig. 1). Each trawl sample was a 5-min tow at 3.4 km/h; based on the width of the trawl when being hauled, each haul covered about 1000 m^2. Samples were collected on two dates near May 1 and weekly from late July to October; spring samples were not collected in May 1968. Perch captured in each haul were counted and age I and older fish were aged from scales.

Catch per unit of effort (CPE) on October 15 was calculated as an index of the abundance of age 0 perch. Because catches of age 0 perch generally declined exponentially from July to October (Forney 1971), CPE on October 15 was estimated from linear regression of the natural logarithms of CPE versus sampling dates. Mean total length of age 0 perch on October 15 was calculated from pooled samples of 25 perch from each site.

Abundance of age I perch on May 1 was estimated as mean CPE for the two spring trawling dates. Mean CPE of age I and II perch during August–September were designated as indices of abundance for September 1.

CPE of age I and II perch in seines was measured to corroborate trawling data. A 22.5-m bag seine with 6-mm mesh in the bag was hauled at nine sites weekly during July 1962–70 (Fig. 1). Sites included areas with rocky, muddy, and sandy bottoms. Samples were collected by extending the seine parallel to shore in water 1 m deep and pulling the seine perpendicular to shore in a U-shape. Mean catch per haul in July was calculated as an index of abundance.

WALLEYE PREDATION

Intensity of walleye predation of age I and II perch was assessed from the frequency of occurrence of perch in stomachs of age III and older walleyes during May–December in 1967–74. Stomachs of age II walleyes also were examined and are included in the analysis for May 1969, the only period in which age I or II yellow perch were observed in age II walleye stomachs. Walleyes captured overnight in gillnet sets and in a benthic trawl hauled shortly after sunrise were weighed, and stomach contents were removed by dissection. Ingested fish were identified as age I or II on the basis of size; 75% of these also were identified to species on the basis of shape and coloration. For samples containing more than 10 identifiable age I and II fish, unidentifiable specimens were apportioned to species and age in the same ratio as identified specimens. For samples containing fewer than 10 identifiable fish, unidentifiable fish were not included in predation estimates.

Estimates of the consumption of age I and II perch by walleyes were based on Bajkov's (1935) formula for calculating daily ration. Total monthly consumption (I) was computed as

$$I = (PB/V)D$$

where

I = monthly number of perch consumed/ha;
P = number of ingested perch/kg walleye examined;
B = kg of age III and older walleyes/ha;
V = evacuation time in d; and
D = d in the mo.

Biomass of walleyes was computed from mark–recapture estimates, growth rates, and distribution of mortality as described by Forney (1967). Evacuation times, based on Hofmann (1972), were 5 d in May, 2 d in July–September, 3 d in October, and 8 d in November–December. Evacuation times are approximations only since Hofmann's experiments used age 0 prey, which would be digested faster than larger age I and II fish (Forney 1977), and force-feeding, which probably decreased evacuation rates (Swenson and Smith 1973). However, similar evacuation times have been reported for other species of large piscivores (Seaburg and Moyle 1964; Hunt 1960).

Results

ABUNDANCE OF YELLOW PERCH COHORTS

Rankings of mean trawl catches for 12 perch cohorts changed at sequential intervals between ages 0 and II

TABLE 1. Relative abundance of the 1962–73 year-classes of yellow perch between ages 0 and II and instantaneous mortality coefficients for the interval age 0 (Oct. 15) to age II (Sept. 1).

Year-class	Trawl catch (number/haul) Age 0 (Oct. 15)	Age I (May 1)	Age I (Sept. 1)	Age II (Sept. 1)	Instantaneous mortality coefficient
1962	435	48.6	19.8	1.7	5.54
1963	78	7.1	2.1	1.0	4.36
1964	496	84.9	72.8	4.2	4.77
1965	260	2.9	0.2	0.1	7.86
1966	15	2.5	3.3	0.9	2.81
1967	210	—	11.2	3.3	4.15
1968	670	59.8	5.5	0.2	8.12
1969	21	0.2	0.1	0.1	6.04
1970	90	15.8	4.4	2.7	3.51
1971	352	5.2	3.3	0.1	9.08
1972	10	0.4	0.1	0.1	5.12
1973	51	6.2	3.6	2.2	3.14

TABLE 2. Mean catch of age I and II perch in seines during July, 1963–70. Number of hauls in parentheses.

Year-class	Seine catch (number/haul) Age I	Age II
1962	24.2 (108)	3.1 (45)
1963	9.8 (45)	0.0 (45)
1964	91.4 (45)	5.3 (72)
1965	5.4 (72)	0.0 (45)
1966	16.4 (45)	0.7 (45)
1967	23.1 (45)	3.6 (36)
1968	15.5 (36)	1.0 (36)
1969	1.5 (36)	—
Correlation (*r*) with mean Sept. trawl catches	0.99	0.93

(Table 1). When perch were age 0, the 1962, 1964, 1968, and 1971 year-classes were the most abundant, but only the 1962 and 1964 year-classes remained abundant at age II. Conversely, the 1970 and 1973 cohorts ranked low in abundance at age 0, but ranked high in abundance at age II. The 1967 and 1970 year-classes, which ranked moderately abundant at age 0, were among the most abundant cohorts at age II.

Catches of perch in seines verified that relative abundance of age I and II perch was accurately reflected by trawl data. Seine catches in July revealed trends similar to trawl catches in August–September (Table 2) despite the fact that trawling was restricted to areas deeper than 4 m and seining to areas shallower than 1 m. Seine data depict 1962, 1964, and 1967 as the most abundant cohorts at ages I and II and 1963, 1965, and 1969 as the least abundant cohorts.

Changes in the ranking of cohorts from when perch were age 0 through age II indicate that mortality rates differed substantially during the interval. Instantaneous mortality coefficients, calculated as the natural logarithm of mean trawl catch at age II divided by mean catch at age 0, varied 3.2-fold among cohorts, indicating two orders of magnitude difference in survival rates during the interval (Table 1). Probable differences between the vulnerability of age 0 and II perch to capture in trawls prevent calculation of actual mortality rates; nevertheless, the instantaneous mortality coefficient should be a reasonable index of relative mortality rates.

Indices of abundance were compared by correlation to identify the interval of major change in cohort abundance (Table 3). A significant correlation between estimates at two periods should indicate no change in relative abundance, whereas a nonsignificant correlation should signify an interval of changing abundance. Data in Table 3 are ambiguous, however, because all consecutive indices are significantly correlated and all nonconsecutive indices are not. A similar set of correlations occurred when indices were transformed to natural logarithms, except that only the correlation between natural logarithms of age 0 and age II indices was nonsignificant. Consequently, a unique interval of year-class modification could not be delineated. While inaccuracy of the indices of abundance may have contributed to this pattern, relative abundance of cohorts may have changed slowly over an extended period. Thus, modifications in abundance which were not detectable between adjacent estimates became apparent across long intervals.

PREDATION ON JUVENILE PERCH BY WALLEYES

Most mortality of age I and II yellow perch in Oneida Lake is probably attributable to predation by walleyes. Death from starvation is improbable because growth of juvenile perch is rapid (Vashro 1975) and because comparison of zooplankton production and consumption by perch suggests that competition for food is negligible (Noble 1975). Mortality attributable to disease or parasitism has not been critically examined, but is presumed small because dead or dying fish were never observed in quantities or concentrations generally associated with epizootics.

Forney (1977) has shown that consumption of age

TABLE 3. Correlation coefficients (*r*) between CPE of yellow perch in trawls at various life stages as shown in Table 1. Number of year-classes in parenthesis; asterisk denotes significant correlation ($P < 0.05$).

Index of abundance	Index of abundance Age 0 (Oct. 15)	Age I (May 1)	Age I (Sept. 1)	Age II (Sept. 1)
Age 0 (Oct. 15)	—	0.82 (11)*	0.49 (12)	0.13 (12)
Age I (May 1)	—	—	0.82 (11)*	0.59 (11)
Age I (Sept. 1)	—	—	—	0.71 (12)*

TABLE 4. Number and weight of walleyes examined annually for prey and total number of age I and II yellow perch observed in stomachs.

	Walleye examined		Number of perch	
Year	Number	kg	Age I	Age II
1967	1154	485.9	25	0
1968	1308	768.8	70	0
1969	975	1549.6	75	0
1970	570	348.1	1	4
1971	1376	747.2	204	1
1972	1359	2164.3	48	7
1973	769	368.9	1	5
1974	1232	1600.0	23	0
Total	8743	8032.8	447	17

TABLE 5. Consumption of age I and II yellow perch (May–December), density of age I perch on May 1 based on the catch and area swept by trawls, and density of walleyes on May 1 based on mark–recapture.

	Yellow perch			
Year-class	Consumed (Number/ha) (a)	Density (Number/ha) (b)	(a)/(b)	Walleye density (Number/ha)
1966	111	25	4.4	28
1967	250	—	—	22
1968	258[a]	598	0.4	24
1969	4	2	2.0	20
1970	349	158	2.2	24
1971	142	52	2.7	24
1972	3	4	0.8	12
1973	39	62	0.6	12

[a] Includes consumption of 20.9 age I perch/ha by age II walleyes in May 1969.

0 perch by walleyes and adult perch accounts for most deaths of age 0 perch between June and October. Cannibalism of age 0 perch ceases in late summer, and no age I or II perch were ever observed in stomachs of adult perch. However, intense predation by walleyes on juvenile perch is expected during the winter and spring, until age 0 perch of the following year-class become vulnerable to walleye predation in mid- to late June.

Stomachs of nearly 9000 walleyes examined during 1967–74 contained few age I or II perch (Table 4). While the low frequency of occurrence indicates that age I and II perch contributed little to the annual diet of walleyes, the importance of walleye predation to perch mortality must be considered relative to the abundance of age I and II perch and the variability of predation among year-classes.

Estimates of the consumption of eight cohorts for May–December when perch were ages I and II varied from 3 to 349 perch/ha (Table 5). Although differences in the density of walleyes presumably contributed to the low consumption of the 1972 and 1973 cohorts, consumption varied 85-fold among six year-classes for which walleye densities were similar.

Consumption estimates for the age I – age II interval are conservative for several reasons. Stomach contents which could not be identified or assigned to species with confidence were not included. Walleye stomachs were not sampled between January and April, when consumption of age II perch probably occurred.

For seven of eight cohorts, estimates of consumption approached or exceeded estimates of the abundance of cohorts based on trawl catches of age I perch on May 1 (Table 5). Consumption estimates greater than abundance are possible because a trawl does not catch all fish in its path. Nielsen (1978) determined that the trawl used in this study captured approximately 10% of adult perch encountered during 1970–73 sampling and 25% during 1969. Because vulnerability of fish to capture probably decreases as size increases, vulnerability of age I perch in spring is likely to be higher than adults. While it is inappropriate to adjust these estimates precisely for vulnerability, the high ratio of consumption to trawl catch implies that a large portion of the mortality of most cohorts was attributable to predation by walleyes.

The relative proportion of a cohort consumed by walleyes varied among cohorts, indicating that consumption was not a simple function of prey density. Ratios of consumption to trawl catch of age I perch in May ranged from 4.4 for the 1966 year-class to 0.4 for the 1968 cohort (Table 5). A portion of this variation is attributable to inaccuracy of the May 1 trawl sampling. Samples consisted of 16–20 trawl hauls, and accuracy is presumably low compared to estimates at other life stages based on 70 or more hauls. However, using trawl catch on September 1 as an index of average abundance throughout the age I year, eightfold variation in the ratio of consumption to trawl catch remained among eight cohorts.

Monthly distribution of consumption showed that walleye predation on age I and II perch was concentrated in the spring. In 5 of 6 yr, more than 60% of all age I and II perch observed in walleye stomachs were observed in May–June (Table 6). Consumption of age I perch in 1972 was distributed throughout the year, perhaps because perch of the 1971 year-class had the shortest mean length of any cohort examined (see below). The general concentration of consumption during spring suggests that older perch were replaced in the diet of walleyes when age 0 perch became vulnerable to predation in mid- to late June.

FACTORS AFFECTING MORTALITY

If predation plays a dominant role in the variation

TABLE 6. Monthly consumption of age I and II perch by walleyes, expressed as a fraction of the total annual consumption.

	Year					
Month	1967	1968	1969	1971	1972	1974
May	0.17	0.52	0.43	0.60	0.13	0.75
June	0.43	0.28	0.38	0.36	0.00	0.00
July	0.12	0.01	0.00	0.02	0.29	0.00
Aug.	0.04	0.03	0.07	0.02	0.04	0.00
Sept.	0.03	0.08	0.06	0.00	0.12	0.25
Oct.	0.04	0.02	0.02	0.00	0.16	0.00
Nov.	0.11	0.03	0.02	0.00	0.13	0.00
Dec.	0.06	0.03	0.02	0.00	0.13	0.00
Total	1.00	1.00	1.00	1.00	1.00	1.00

of mortality among year-classes, mortality coefficients should vary in relation to factors which modify predation. Based on typical predator–prey relationships and previous research regarding walleye predation, mortality coefficients were compared to densities of predators and prey, density of primary prey (Forney 1974), and length of perch (Chevalier 1973; Parsons 1971).

Variation in the abundance of predators should affect total consumption of prey, but the data show no apparent relation between perch mortality and walleye density (Table 7, Fig. 2A). Because density of walleyes was relatively constant in most years, evidence of a relationship presumably was masked by relatively large changes in other factors, such as abundance of alternate prey and size of perch (see below). Mortality rates were lower for the 1972 and 1973 cohorts, both of which were exposed to predation by walleye populations of unusually low density.

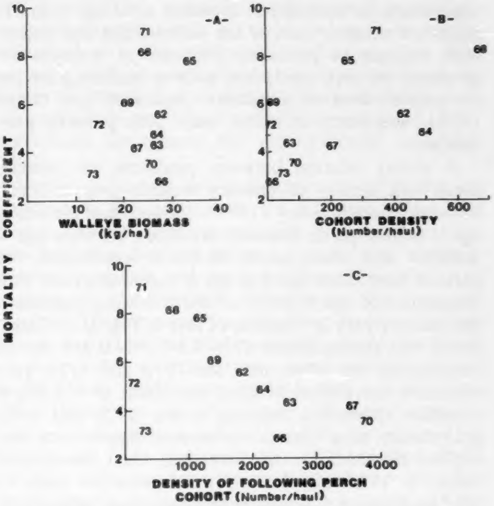

FIG. 2. Instantaneous mortality coefficients of yellow perch cohorts from age 0 (Oct. 15) to age II (Sept. 1) as a function of (a) walleye biomass (kg/ha), (b) cohort density as age 0 on Oct. 15 (catch/haul), and (c) density of following year-class of perch as age 0 on Aug. 1 (catch/haul).

A positive relationship existed between mortality coefficients and density of the cohort in October at age 0 (Table 7, Fig. 2B). Correlation was significant ($r = 0.58$, $P < 0.05$), but substantial variation suggests that density of juvenile perch exerted a relatively small influence on predation rate. The lack of strong density-

TABLE 7. Relative instantaneous mortality coefficients of perch cohorts between age 0 (Oct. 15) and age II (Sept. 1) compared with biomass of walleyes when perch were age I (May 1), perch cohort density when age 0 (Oct. 15), density of primary walleye prey (age 0 perch of following cohort on Aug. 1), and lengths of perch at age 0 (Oct. 15) and age I (Sept. 1).

Year-class	Instantaneous mortality coefficient	Walleye biomass (kg/ha)	Perch cohort density (number/haul)	Density of following perch cohort (number/haul)	Mean perch length (mm)	
					Age 0	Age I
1962	5.54	28	435	1850	73.5	120.3
1963	4.36	27	78	2596	61.2	—
1964	4.77	27	496	2168	70.4	115.8
1965	7.86	34	260	1197	60.9	—
1966	2.81	28	15	2447	70.7	—
1967	4.15	23	210	3599	72.9	130.8
1968	8.12	25	670	720	67.6	129.2
1969	6.04	21	21	1401	63.1	—
1970	3.51	26	90	3772	75.5	141.3
1971	9.08	25	352	253	58.0	121.1
1972	5.12	15	10	120	65.7	—
1973	3.14	13	51	315	86.1	156.2

dependence in mortality is expected since age I and II perch are a minor part of the walleye diet and behavioral changes in predatory behavior of walleyes responsible for such a relation, such as searching images or concentration of predators (Murdoch and Oaten 1975), are likely to occur only with primary prey species.

A strong relation between predation on juvenile perch and density of primary walleye prey is likely, however, since Forney (1974) showed that abundant age 0 yellow perch buffered predation on both age 0 walleyes and white perch. Mortality coefficients for perch cohorts from age 0 to age II varied inversely with abundance of age 0 perch of the following year-class, the primary prey of walleyes (Table 7, Fig. 2C). Correlation was nonsignificant ($r = 0.54$, $P > 0.05$) for 12 year-classes, but when data for 1972 and 1973 were excluded, correlation became significant ($r = 0.89$, $P < 0.05$). Conditions relating to the 1972 and 1973 year-classes were unusual in several regards and may explain the deviation of these data from the general trend. In 1973, age 0 white perch were six times as abundant as age 0 yellow perch; therefore, densities of primary prey buffering predation on the 1972 cohort of age I yellow perch were approximately seven times greater than shown. Predation on the 1973 cohort of juvenile yellow perch was low presumably because density of walleyes was lower and size of perch was higher than in any other year.

Because walleyes are size-selective predators, length of perch should affect mortality rates if predation is a principal cause of mortality. Lengths of age I and older perch found in walleye stomachs indicate that maximum length of perch eaten is about 40% of predator size (Fig. 3). Because adult walleyes in Oneida Lake consistently range 300–500 mm in length (Forney 1965), yellow perch outgrow vulnerability to walleye predation while growing through the 120–200 mm length range. This range corresponds to the lengths of perch during the second growing season (Table 7). Thus, year-classes containing rapidly growing fish should be subject to predation for a relatively short interval and incur lower mortality rates than year-classes with slow growth.

Mortality coefficients were inversely related to mean lengths of age I perch on September 1 for seven cohorts (Table 7, Fig. 4A). Adequate data for calculating growth of age I perch were available only for seven cohorts, but significant correlation between mean lengths of age 0 perch in October and age I perch in September for these cohorts ($r = 0.76$, $P < 0.05$) indicates that length of age 0 perch in October was a reliable index of relative length throughout the age 0–age II period. The inverse relation between mortality coefficients and mean lengths of age 0 perch for 12 cohorts was similar to that for lengths of age I perch (Table 7, Fig. 4B). Correlations were significant between mortality and lengths of both age 0 and age I perch ($r = 0.68$ and 0.81, respectively, $P < 0.05$).

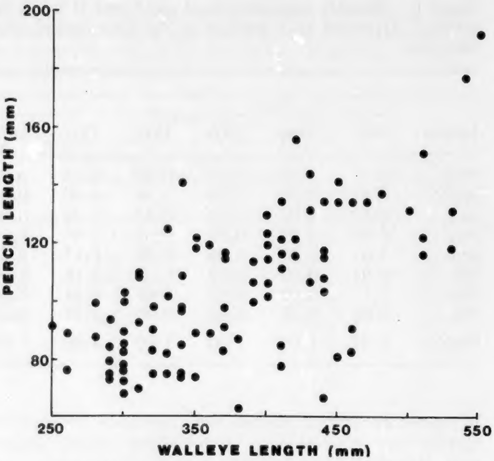

FIG. 3. Lengths of age I and older yellow perch recovered from stomachs of walleyes.

The relations between instantaneous mortality coefficients and combinations of the factors considered above were tested in sequential multiple regressions. Variables were added to the regressions in the order of the magnitude of the simple regression coefficients, and significance was determined by analysis of variance. For 12 cohorts, significant variables in the multiple regression were mean length of age 0 perch in October (X_1), density of age 0 perch on October 15 (X_2), and numerical density of the following perch cohort on August 1 (X_3). The regression equation is

$$Y = 15.403 - 0.145X_1 + 0.004X_2 - 0.001X_3$$

where Y = instantaneous mortality coefficient between age 0 on October 15 and age II on September 1. The regression explained 85% of the variation in mortality coefficients for 12 year-classes.

When data for the 1972 and 1973 cohorts were excluded, the form of the multiple regression depended on the order in which variables were added to the regression. When variables were added in the same order as in the regression for 12 cohorts, abundance of alternate prey was not a significant variable ($R^2 = 0.80$, using perch length and density). However, if abundance of alternate prey was the first variable in the regression, perch length and density became insignificant variables ($R^2 = 0.79$, using density of alternate prey).

Discussion

Predation on age I and II perch contributed to variation in perch mortality rates, influencing eventual recruitment to the fishable and reproductive populations in Oneida Lake. Although precision of the relationship

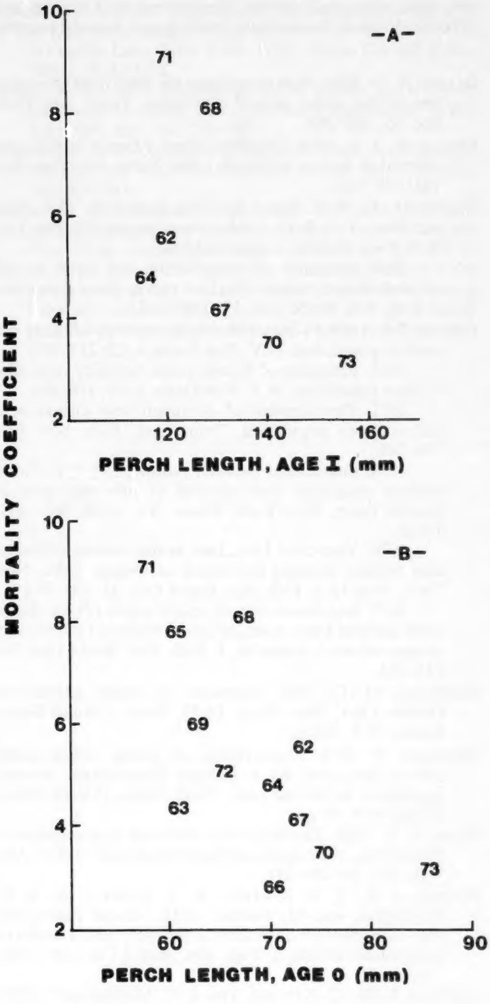

FIG. 4. Instantaneous mortality coefficients of yellow perch cohorts from age 0 (Oct. 15) to age II (Sept. 1) as a function of (a) mean length of age I perch on Sept. 1 and (b) mean length of age 0 perch on Oct. 15.

between consumption and abundance is low, characteristics of the sampling suggest that predation on juvenile perch may be more important than shown with these data. Samples used for this study were collected from demersal habitats in which age 0 and adult perch are abundant. Casual observations based on catches of perch in seines and trawls, however, suggest that age I and II perch are concentrated in littoral areas. Ryder and Kerr (1978) noted that yellow perch in shallow water become lethargic at night and may be highly vulnerable to walleyes foraging in littoral areas. Presumably, walleye predation on age I perch should be higher in littoral than in demersal areas if denser concentrations of prey allow walleyes to select for larger prey items throughout the year (Werner and Hall 1974).

Studies depicting the importance of predation on late-juvenile fish are rare in the literature. Ward and Larkin (1964) demonstrated that predation by rainbow trout on 2-yr-old sockeye salmon was inversely density-dependent and produced dominant cohorts of sockeye at 4-yr intervals. Mortality of the Japanese cyprinid *Gnathopogon caerulescens* during the first winter was a function of density and caused reordering of the relative abundance of cohorts between ages 0 and I (Maki 1968). It is probable that variable mortality during late-juvenile stages influences year-class strength in many populations, but difficulty of sampling presumably restricts investigation of this period. Data for this study, for example, were developed primarily from research designed to sample age 0 perch, and the tentative nature of data regarding such characteristics as growth of age I perch, digestion rates of large prey, and abundance of perch in spring affects the confidence with which interpretations are made.

Changes in the relative abundance of perch cohorts between ages 0 and II conflict with the generalization that year-class strength is determined during egg and larval stages. Such changes have several implications for research and management. First, studies in which relative abundance of adult fish is correlated with factors influencing survival during embryonic or larval stages may indicate coincidental rather than cause–effect relationships. A model by Koonce et al. (1977) which related percid year-class strength to temperature failed to describe accurately the abundance of yellow perch in Lake Erie despite the fact that many studies have shown significant correlation between abundance and temperature. Such correlations should be interpreted with caution unless the underlying mechanisms have been defined. Second, larval or fingerling surveys may be unreliable as indices of the future abundance of a cohort at reproductive or exploitable age. Estimation of juvenile abundance may be more reliable, provided that adequate sampling procedures can be developed. Third, management designed to alter the mortality rate of juveniles may yield substantial benefits in terms of more abundant or more stable populations of adult fish. Desirable management may include introducing invertebrates or increasing primary production to increase growth rates of prey, providing alternate prey to buffer predation, or manipulating the environment to create or destroy prey refuges.

This and other studies of juvenile perch in Oneida Lake demonstrate that abundance of perch cohorts at age III is determined principally by noncompensatory mortality. Clady (1976) showed that mortality from the egg to the larval stages was related to density-independent factors of wind velocity and water temperature. During the remainder of the first year, mortality of perch was caused by walleye predation and was inversely density-dependent (Forney 1971). This analysis suggests that predation rates, as modified by perch length, perch density, and abundance of alternate prey, determined rates of mortality of age I and II perch. The consequence of noncompensatory mortality is large fluctuation in year-class strength typical of yellow perch populations in Oneida Lake and elsewhere.

Compensatory mortality during the juvenile interval might occur, however, at densities higher than those observed in this study. If age I or II perch became a major portion of the walleye diet, the foraging behavior of walleyes might be influenced directly by density of juvenile perch. Although growth of perch in Oneida Lake has been independent of density (Noble 1975; Vashro 1975; Nielsen 1978), higher densities of age I and II perch could trigger compensatory growth. Abundant cohorts, growing slowly, would be vulnerable to predation for relatively longer periods and have higher mortality rates.

Complex patterns and causes of mortality, as demonstrated for yellow perch and walleye in Oneida Lake, also have been identified in regulation of the abundance of *Perca fluviatilis* in Lake Windermere (Le Cren et al. 1977, 1972). Such interactions indicate that simple models cannot explain or predict the response of percids to an altered environment or fish community or the structure of percid communities across broad habitat or geographic ranges. Regier et al. (1969) suggested that predator–prey interactions among percids were not inherent to the species involved, but depended largely on the specific situation. Ryder and Kerr (1978) developed this idea by conceptualizing the integrity and persistence of percid communities as a bell-shaped curve reaching the maximum in mesotrophic waters. Percid communities appear to be especially vulnerable to instability in structure and function because of overlap with salmonid communities in oligotrophic waters such as Windermere and with centrarchid communities in eutrophic waters such as Oneida and Lake Erie. Plasticity of community interactions may explain the multitude of factors advanced by various authors to explain the abundance of percid populations. Clearly, adequate understanding of particular percid communities relies on the direct study of interactions among populations, particularly those involved in predator–prey interactions, at all stages of development.

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Terebellidae (Polychaeta) from the Northeast Pacific Ocean[1,2]

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BANSE, K. 1980. Terebellidae (Polychaeta) from the Northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 37: 20–40.

Betapista dekkerae, new genus and new species, is described. The generic diagnoses for *Laphania* and *Scionides* are improved after inspection of the holotypes of the type species. *Eupolymnia heterobranchia* (syn., *E. crescentis*) is redescribed. Additions to the descriptions, based on study of type material, are made for *Laphania boecki* (new record, Northeast Pacific), *Neoamphitrite robusta* (syn., *Scionides dux*), *Neoleprea californica* and *N. spiralis*, *Pista brevibranchiata* (new record, British Columbia [B.C.], Washington [WA], Japan) and *P. fratrella*, and *Polycirrus californicus* (new record, B.C., WA; syn., *P. perplexus*). Other additions to the descriptions are provided for *Amaeana occidentalis* (new record, B.C.) and *Pista cristata*. Two further *Pista* species (one from the Skagerrak) and five *Polycirrus* species are charcterized but not named. Other new records are *Lanassa venusta venusta* (B.C.), *Lysilla loveni*, and *Neoleprea japonica* (the two latter for Northeast Pacific). *Lysilla pacifica*, *Pista fasciata*, and *P. fratrella* are shown not to be members of the fauna of British Columbia and Washington. Presumably, neither is *Polycirrus caliendrum*. New observations on the types of the Antarctic *Polycirrus kerguelensis* and *Ereutho kerguelensis* are noted.

Key words: Betapista n.g., *Neoleprea*, new records, Northeast Pacific, *Pista*, *Polycirrus*, *Scionides*, Terebellidae

BANSE, K. 1980. Terebellidae (Polychaeta) from the Northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 37: 20–40.

Nous décrivons *Betapista dekkerae*, nouveau genre et nouvelle espèce. L'inspection des holotypes de l'espèce type nous permet d'améliorer la diagnose générique de *Laphania* et *Scionides*. Nous redécrivons *Eupolymnia heterobranchia* (syn., *E. crescentis*). Après étude du matériel type, nous ajoutons aux descriptions de *Laphania boecki* (mention nouvelle, Pacifique Nord-Est), *Neoamphitrite robusta* (syn., *Scionides dux*), *Neoleprea californica* et *N. spiralis*, *Pista brevibranchiata* (mention nouvelle, Colombie-Britannique [C.-B.], Washington [WA], Japon) et *P. fratrella*, et *Polycirrus californicus* (mention nouvelle, C.-B., WA; syn., *P. perplexus*). Nous faisons également d'autres additions aux descriptions d'*Amaeana occidentalis* (mention nouvelle, C.-B.) et *Pista cristata*. Nous donnons les caractéristiques de deux autres espèces de *Pista* (dont l'une du Skagerrak) et de cinq espèces de *Polycirrus*, mais ne les nommons pas. D'autres signalements nouveaux sont *Lanassa venusta venusta* (C.-B.), *Lysilla loveni* et *Neoleprea japonica* (ces deux derniers dans le Pacifique Nord-Est). Nous démontrons que *Lysilla pacifica*, *Pista fasciata* et *P. fratrella* ne font pas partie de la faune de la Colombie-Britannique et de l'Etat de Washington. Il en est probablement de même de *Polycirrus caliendrum*. Nous mentionnons de nouvelles observations sur les types des espèces antarctiques *Polycirrus kerguelensis* et *Ereutho kerguelensis*.

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THE Oregon Biogeographic Province comprises the fauna of the Northeast Pacific continental shelf between Point Conception, California, to the south, and Dixon Entrance, approximately at the southern tip of southeast Alaska (Briggs 1974). Within the Province, the polychaete fauna is best known in British Columbia and Washington. The family Terebellidae, however, has never been treated monographically in the region except that summaries are available in the form of keys (Berkeley and Berkeley 1952, for British Columbia; see also Hartman 1969, for northern California). In consequence, the family remains incompletely known in the Province although many of its members may be several centimetres long and/or be conspicuous because of their striking color. The purpose of this paper is to

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improve on the situation by rectifying old records and reporting on new collections.

The following numbers indicate the present degree of faunistic and taxonomic knowledge of the Terebellidae of the Oregon Province: 33 species have been recorded from British Columbia and Washington, and 10 additional species have been found off Oregon and northern California (cf. Hartman 1969; K. D. Hobson and K. Banse unpublished data). Of those 33 species only one is new to science, but 12 are new records for British Columbia or Washington and are presented here. Two of the 12 faunistic additions are a result of taxonomic revisions but do not change the number of species recorded. Five, belonging to the genus *Polycirrus*, cannot be named because of the taxonomic disarray within this genus; at least four of these are newly reported for the Province. Of the remaining five new records, three species were previously known only outside the Province.

In the following species descriptions, the thoracic segments are numbered such that the first gill is ordinarily inserted on segment 2, and the first segment with nephridia is segment 3. For the sake of brevity, the distinction between nephridia proper and gonoducts is not made.

Amaeana Hartman

Amaeana occidentalis (Hartman)

Fig. 2A

Amaea occidentalis Hartman, 1944:277.
Amaeana occidentalis — Hartman 1959:495; 1969:581.

MATERIAL: British Columbia: So. side of Barkley Sound, Erin I., 48°55.5′N, 125°15.7′W. Solid rock out-cropping from sand/gravel, 15 m, Aug. 7, 1973. B. Cooke and P. Lambert coll., K. D. Hobson ident. (BCPM[3] 973-194-12N, 5 specimens). — Barkley Sound, Treble I., between Nettle and James I., sand-shell slope, 9–12 m, Aug. 14, 1973. K. D. Hobson ident. (BCPM 973-235-40, 1 specimen).

ADDITION TO THE DESCRIPTION: The specimens are well-preserved, and agree with the description by Hartman (1944). To the description may be added that the thoracic notosetae (present on 12 segments) are arranged in two series. In the largest specimen, almost 3 cm long (without tentacles), 15–20 setae occur in each series in a median parapodium. The tips of the shorter setae barely emerge from the parapodia and do not extend beyond the edge of the parapodial lappets. In the larger setae, about one-quarter of the total length emerges, and the tips of the setae are freely visible. All setae are finely hirsute to the tips. The hairs, which are spaced about 1 μm apart, are easily visible only in the optical longitudinal section (Fig. 2A). Careful study shows that they are arranged around the entire seta.

REMARK: Wollebaek (1912) and Day (1973), inter alia, described "small" (Wollebaek) or "poorly defined" (Day) ventral shields for *Amaeana trilobata* (Sars), which are lacking in *A. occidentalis* according to Hartman (1944). However, it seems from the present material that the ventral furrow observed by her can be contracted in a variable manner. As a result, segmental "ventral shields" appear to be present anteriorly, or in the setae-free median region, or in the abdomen.

New record. The known distribution of the species is extended from central and southern California to southern British Columbia.

Betapista new genus

DIAGNOSIS: A member of the Terebellidae with pronounced lateral lappets and ventral shields. With 3 pairs of arborescent gills from segment 3. Notosetae smooth, from segment 4, on 17 segments. Long-handled uncini from segment 5; uncini in double rows from segment 11. With 3 pairs of posterior nephridia.

TYPE SPECIES: *Betapista dekkerae* new species.

The name of the genus refers to the provisional name, *Pista* B, given by K. D. Hobson.

DISCUSSION: The new genus is a member of the Amphitritinae. The smooth notosetae, the long-handled uncini in anterior segments, and the lateral lappets suggest that it is closely related to *Eupistella* Chamberlin, *Lanicides* Hessle, *Opisthopista* Caullery, and *Pista* Malmgren (including *Axionice* Malmgren which, like *Pista*, have uncini with thin posterior handles in the type species, see Hessle 1917:153). *Betapista* is remarkable among the Terebellidae by the distribution of gills over the anterior segments. Ordinarily among the family members with three pairs of gills, the first pair inserts on segment 2 and the third on segment 4 (first setiger). An example of the few exceptions is *Terebellobranchia* Day which has three pairs of branchia at intervals over the thorax. Only *Terebellanice* has been described as having gills on segments 3–5 (Hartmann-Schröder 1962); however, the genus was erroneously based on a species of *Thelepus* Leuckart (G. Hartmann-Schröder, Zool. Museum, University of Hamburg, in litt.). The gills thus are found on segments 2–4; and while *Thelepus* is a member of the Thelepinae, *Betapista* clearly belongs to the Amphitritinae.

For the establishment of the new genus, the correct numbering of segments is salient. Since dissection and location of the principal dissepiment is not possible, the following may be mentioned: The counting of segments in *Betapista* may be based on the beginning of the double rows of uncini on segment 11, a diagnostic character at the level of the subfamily (see Hessle 1917:145; Caullery 1944, for *Opisthopista*); or it may be based on the nephridial papilla which is probably present on segment 3 (in homology with *Eupistella*

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[3] For abbreviations, see Acknowledgments.

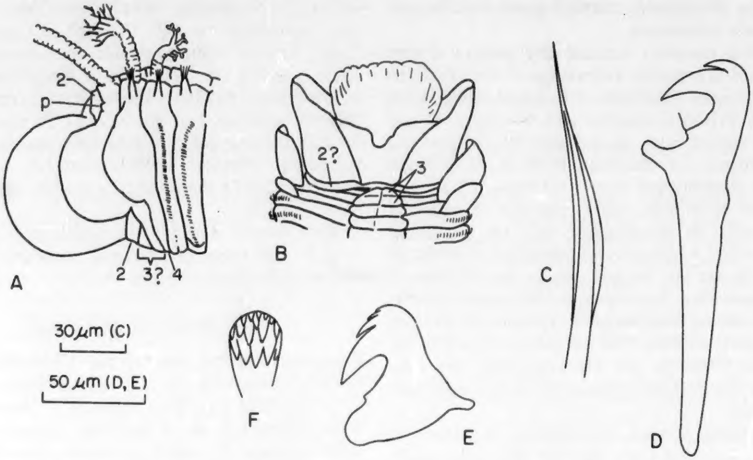

FIG. 1. *Betapista dekkerae*, new species: A, anterio-lateral view [schematic, composite of right and left sides; tentacles omitted; numbers indicate segments; p, nephridial papilla]; B, anterior end, ventral view; C, notoseta from setiger 2; D, uncinus from setiger 2; E, F, uncinus of setiger 15, side and frontal views (all holotype).

[as *Eupista*] and *Pista*, see Hessle 1917); or it may rely on the recognition of annuli (see Fig. 1A, dorsally, and the questionable interpretation ventrally; also Fig. 1B). All these criteria indicate that the first pair of gills inserts on segment 3 in *Betapista*.

Whether all of the characters given in the diagnosis of *Betapista* are valid generic characters cannot be known until further material is available. In the related *Pista*, the number of pairs of gills varies among species, and the number of gills on any segment may change within species. Similarly the number of posterior nephridia possibly varies among species in a related genus: there are usually two within *Pista* (also in *Lanicides* and *Eupistella*, as far as known), but *P. cretacea* (Grube) and *P. atypica* Hessle (*nomen est omen*?) have many more. It is likely, however, that the number of segments with notosetae and the arrangement of lateral lappets over the anterior segments are only specific characters within the new genus, considering the situation within *Pista*.

Betapista dekkerae n.sp.
Fig. 1

DIAGNOSIS: A species of *Betapista* with lateral lappets on segments 1, 3, and 4. With 17 thoracic setigers. Last three without ventral shields.

The species is named after the late Katharine Dekker Hobson who recognized the type specimen as an unusual, *Pista*-like form.

HOLOTYPE: British Columbia, Blubber Bay, 49°48.2′N, 124°37.1′W, clayey sand, 25–35 m, Dec. 8, 1965. D. V. Ellis coll., K. D. Hobson ident. as *Pista* B. (BCPM 978-174-1).

MATERIAL: Holotype.

DESCRIPTION: The holotype is a well-preserved anterior fragment, with 17 thoracic setigers and 2 abdominal segments, of about 1.2 cm length. Approximately five tentacles each are attached on both sides of the prostomium, laterally to the upper lip. In lateral view, the upper lip is hidden by a large fold inserted on segment 1 (Fig. 1A). This fold is constituted of a pair of thick lateral folds which are united ventrally by abruptly thinned, but not transparent, tissue which is incised midventrally (Fig. 1B). Two pairs of smaller lateral folds insert on segments 3 and 4.

Segmental borders are distinct in the anterior thoracic setigers but disappear posteriorly. Dorsally, in the anterior thorax, the segments each are subdivided into approximately five annuli which are crossed by irregular longitudinal folds giving the epidermis a rugose appearance under 50× magnification. On the underside of the thorax, broad ventral shields are present except in the last three setigers (15–17). Figures 1A, B illustrate the interpretation of the segmentation: Dorsally a ring anterior to the segment bearing the first pair of gills is clearly separate from the dorsal end of the lateral fold on segment 1 (being dorsal and posterior to it); the ring is incised in the midline. Further evidence for the first gill-bearing segment being segment 3 is shown by the structure below the gills which I regard as a nephridial papilla. Ventrally, the interpretation is less conclusive: the first ventral shield appears to be on segment 3 but an anterior and posterior part can be weakly discerned (Fig. 1A, B) in contrast to the following ventral shields. Therefore, the first shield may belong to two segments.

Arborescent gills originate on segments 3–5 and are of unequal size. The first pair carries towards the distal end secondary branches which in turn divide a few (2–3?) more times. The second pair of gills which is shorter than the first has the secondary branches similarly arranged (Fig. 1A). The third gill-bearing segment carries only a small gill on the right side.

Notopodia occur from segment 4 through 17 segments; long tori are present from segment 5. The notosetae are smooth and limbate (Fig. 1C). Uncini of the first torus have broad and long handles (Fig. 1D); in frontal view they possess 3–4 small teeth above the main tooth, and sometimes a single small tooth above those. The uncini are arranged in double rows from setiger 8 through the last thoracic segment. Uncini on setiger 15 carry 6 (7?) small teeth above the rostrum (frontal view) with several smaller teeth inserted above; the posterior handle is reduced to a knob (Fig. 1E, F). The abdominal tori are about half as long as the last thoracic ones. Their uncini were not dissected for study.

Nephridial papillae, other than that on segment 3 insert on the segmental borders behind the notopodia 4–6. The color of the preserved specimen is pink.

Eupolymnia Verrill

Eupolymnia heterobranchia (Johnson)

Fig. 2B–E

Lanice heterobranchia Johnson, 1901:427 — Moore 1909:270 — Hessle 1917: 178 — Rioja 1947:210.
Eupolymnia heterobranchia — Berkeley 1929:310 — Berkeley and Berkeley 1950:63; 1952:88 — Hartman 1959:504; 1961:40; 1969:592 — Dales 1961a:168; 1961b:307.
Eupolymnia crescentis Chamberlin, 1919b:265 — Berkeley and Berkeley 1941:53 — Rioja 1941:731 — Hartman 1938:17; 1944:271; 1948:44; 1959: 504; 1961:40; 1969:591 — Hartman and Reish 1950:45.

MATERIAL: British Columbia: East side of Griffith Harbour, on sand, July 19, 1974. K. D. Hobson coll., ident. (BCPM 974-256-16, 2 specimens). — Parsons Bay, April 20, 1966. D. B. Quayle coll., ident. (BCPM 974-587-1, 4 specimens). — Barkley Sound, Vancouver I. (Sta. 10 N). P. Lambert coll., K. D. Hobson ident. (BCPM 973-153-10, 1 specimen).

Washington: San Juan Island, Lonesome Cove: at low tide level; May 25, 1967. G. Lambert coll. (FHL 1175, 2 specimens); Turn Point, intertidal, July 25, 1960. R. Dales and G. Johns coll., ident. (FHL 254, 1 specimen).

California: Crescent City, 1859 or 1860. A. Agassiz coll. (MCZ 2035, holotype, and MCZ 449, paratype [dried] of *E. crescentis*).

HOLOTYPE: The type material of *E. heterobranchia* consisted solely of the holotype, an incomplete specimen. It was collected during the last century in Washington waters but the exact locality and depth are unknown. The holotype originally was deposited in the Columbia University collections but it is no longer there. In 1975, it could not be found in the American Museum of Natural History, New York, where some of Johnson's types are kept now, nor in the collections of the Museum of Comparative Zoology, Cambridge, where Johnson deposited much of his material, nor the Museum of the Academy of Natural Sciences, Philadelphia, nor the U.S. National Museum of Natural History. Therefore, the holotype can be presumed lost.

REDESCRIPTION: Animals from British Columbia are up to 13 cm long. The longest possesses 68 setigers followed by the regenerating posterior end of small diameter with developing setigers. The holotype of *E. crescentis* has about 85 setigers plus a regenerating posterior end of another 16 setigers, and measures 11 cm. Animals from the intertidal of San Juan Island, within 15–80 km from any of the possible type localities, are somewhat smaller.

Typically, in animals from British Columbia and Washington, the body is thickest anteriorly and tapers gradually through the anterior abdomen. The middle and posterior sections of the abdomen are of about uniform thickness. The dorsal region of the thorax is low past the insertion of the third pair of gills where it rises abruptly. From there the dorsal surfaces of the thoracic and abdominal segments are clearly divided into anterior and posterior rings which in turn are subdivided by parallel lines.

The lip above the mouth is large and has a smooth, gently undulating edge. Between it and the low, collar-like tentacular lobe originate the very numerous, long tentacles which all appear to be of one kind. On the posterior face of the tentacular lobe is a narrow band of purple eyespots stated to be absent by Johnson (1901). The lip below the mouth also has a smooth edge.

The conspicuous latero-ventral folds of the first gill-bearing segment are connected midventrally. The two following segments have thick lateral folds. The folds on all three segments are about half as wide as the segments are long. The lateral, anterior edges of the ventral shields of the two following segments (the first uncinigers) have a macroscopic structure similar to the lateral folds. The ventral shields are large except in the last thoracic segments (Fig. 2B). The anterior shields are incompletely subdivided by longitudinal folds.

On each side, the gills are inserted more or less on a line that converges slightly towards the anterior end. The first pair is markedly larger than the second and

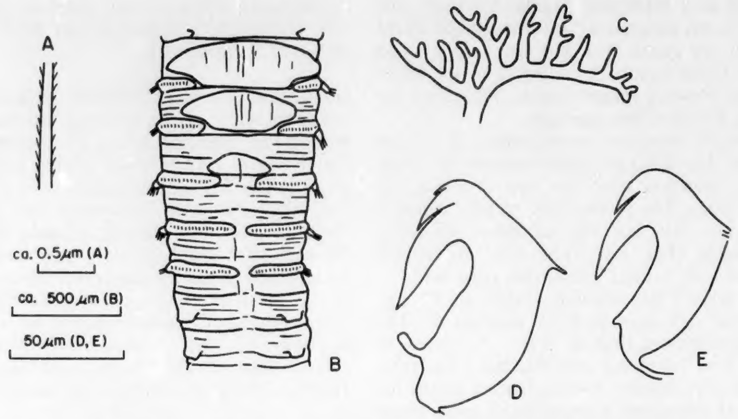

FIG. 2. *Amaeana occidentalis*: A, detail of notoseta. *Eupolymnia heterobranchia*: B, last thoracic and first abdominal segments, ventral view [setae schematic]; C, distal end of gill [only blood vessel drawn]; D, E, uncini from middle of tori in middle thorax and middle abdomen (B–E, Washington).

third pairs but even so is somewhat shorter than the body is wide. In all, the trunk is strong (cf. Johnson 1901, pl. 17, fig. 172). The terminal branches are very short, relative to the length of the total gill, and originate in series rather than dichotomously (Fig. 2C). Because of this mode of branching, the terminal end as a whole tends to form a whorl or spiral. The entire gill is compact.

The first, of in all 17, large notopodia insert on the third gill-bearing segment. Thoracic setae are arranged in two series and are bilimbate (see Johnson 1901, pl. 17, fig. 173). Uncinigerous tori are present from the second setiger. In the posterior thorax, the tori on each side gradually extend to the ventral surface of the body until they almost meet in the last two thoracic segments. The very short abdominal tori form lappets which in the posterior abdomen are almost twice as long as in Fig. 2B. Uncini are arranged in double series from the 8th through the 17th setigers. The thoracic (Fig. 2D) and abdominal (Fig. 2E) uncini are similar except that the base of the former is broader; also, the latter are supported by strong chitinous threads. Ordinarily, there are two large teeth above the rostrum, with a third small tooth inserted above and between them. Occasionally, one can see a tiny tooth on the side of this middle tooth. In some uncini, within the same torus, there may be only one tooth above the main fang, or the mentioned third tooth is bifid, or the single third tooth is as large as the paired ones so that three teeth of equal size appear above the rostrum, more or less side by side.

Nephridial papillae insert below the second gill, and behind and below the first and second notopodia. The body color is ordinarily red-brown but the holotype of *E. crescentis* is grey-green. Large specimens from British Columbia carry innumerable elliptical eggs of up to about 0.35 mm × 0.2 mm size, with a much shorter, third axis so that the eggs are flat. The tube of the holotype of *E. heterobranchia* was made of mud (Johnson 1901), whereas that of the paratype of *E. crescentis* and that of the British Columbia material is constructed of coarse material.

There is variability in some characters. The gills can vary markedly: those of the holotype of *E. crescentis* are very similar to the above description; those of sample 974-587-1 from British Columbia, however, have few and very thick terminal branches, of a lower order but of the same pattern of branching. In one of these animals the first pair of gills has a stem somewhat longer than the body is wide. The stem is filled with dark blood so that this specimen may demonstrate the expanded position of the gills.

Among eight animals in which the notopodia were counted, only four have 17 pairs; one has 17 and 18 notopodia; one has 16 and 17; and two animals each have 16 and 18 pairs of notopodia, respectively. There may be only one thoracic setiger without ventral shields (in small as well as large specimens). The dorsum of the thorax may appear rugose.

The proportion of thoracic uncini that lack paired large teeth above the rostrum is variable: within a torus, one-third to almost one half of the uncini may be equipped with only one large tooth above the rostrum, above which two small teeth are found (e.g. holotype of *E. crescentis*). Abdominal uncini of specimens from British Columbia usually have two teeth above the rostrum, but a few uncini in a torus may have three.

Remarks: *Eupolymnia crescentis* was very tentatively regarded as identical with *E. heterobranchia* by Hartman (1959, 1969). The study of the present material, as well as the available descriptions, show that there are no distinguishing diagnostic characters; therefore, *E. crescentis* is placed in synonymy with *E. heterobranchia*.

Eupolymnia heterobranchia is common in the northeastern Pacific and is distinguished from the other cool-temperate North Pacific species of *Eupolymnia*, *E. congruens* (Marenzeller), *E. nebulosa* (Montague), and *E. trigonostoma* (Schmarda) [for the latter species, see Imajima and Hartman 1964], by the lower number of nephridial papillae and hence nephridia (three instead of six, see Hessle 1917). Moreover, *E. nebulosa* has large lateral lappets (see Hessle 1917) and *E. congruens* has clearly dichotomously-branched gills (see Marenzeller 1884).

While the previously known range of the species extends from Shelikov Strait, west of Kodiak Island (Gulf of Alaska, Hartman 1948) to western Mexico (Berkeley and Berkeley 1952; Hartman 1969), the collections of the American Museum of Natural History, New York, contain specimens identified by A. L. Treadwell (as *Laonice* [sic!] *heterobranchia*) from Bering Strait (Nos. 1637, 1646). I, however, have not seen these specimens.

Lanassa Malmgren

Lanassa venusta venusta (Malm)

Laphaniella venusta Malm, 1874:98.
Lanassa venusta — Hessle 1917:205 — Hartman 1959: 506 — Banse and Nichols 1968:226.
Lanassa venusta venusta — Ushakov 1955:397.

Material: British Columbia: Drew Harbor, sand, 25 m, Dec. 6, 1965. D. V. Ellis coll., K. D. Hobson ident. (BCPM 43, 1 specimen).

Remarks: In the North Pacific Ocean, the nominal subspecies previously was recorded from the Bering Sea (Ushakov 1955) and Puget Sound (Banse and Nichols 1968). The latter authors, however, did not use trinomial nomenclature. The present specimen adds a new record to the fauna of British Columbia.

Laphania Malmgren

Laphania Malmgren, 1866:386 — Wollebaek 1912:74 — Hessle 1917:203 — McIntosh 1922:162 — Fauvel 1927:269 — Ushakov 1955:395 — Fauchald 1977:131.

Diagnosis: A member of the Terebellidae without pronounced lateral lappets, with distinct ventral shields. Without gills. Notosetae smooth, from segment 3, on 17 segments. Uncini with small posterior handles, from segment 9; in double rows from segment 11. Anterior nephridium reduced; posterior nephridia free, on segments 5–8.

Type Species: *Laphania boecki* Malmgren.

Remarks: The present diagnosis is a paraphrase of previous ones but adds one character: uncini with small posterior handles. Also, the confusion about the arrangement of the uncini in posterior thoracic segments, incorrectly reported by Hessle (1917), McIntosh (1922), and Fauvel (1927), is rectified.

Laphania seems to be the only known terebellid genus to combine a lack of gills with long-handled uncini. The character is also of interest because it has been noted in only one other genus without distinct lateral lappets (*Hadrachaeta* Hutchings). The occurrence of long-handled uncini is used prominently in every terebellid key, but Hessle (1917:145) already regarded these uncini as a diagnostic character of little value within the family (i.e. being in his opinion a character of low phylogenetic importance); he emphasized instead the value of lateral lappets.

The fold surrounding segment 2 may actually be a diagnostic character on the generic level. On the other hand, the inclusion of the number of thoracic segments in the generic diagnosis may turn out to be unwise as Ushakov (1955) recorded a *Laphania* sp. with 14 (15?) thoracic setigers (see, however, the observations on the low number of notopodia in juveniles of *L. boecki* reported below).

Laphania boecki Malmgren
Fig. 3A, B

Laphania boecki Malmgren, 1866:386; 1867:219 — Ditlevsen 1911:429 — Wollebaek 1912:73 (footnote), 134 (plates) — Hessle 1917:204 — McIntosh 1922:163 — Fauvel 1927:269 — Ushakov 1955:396 — Hartman 1959:507.

Material: Skandinavia: Finmark, without exact locality or date (SMNH 6711, holotype).

British Columbia: Bank I., White Rocks, 53°35.1'N, 130°34.9'W, shell-gravel, intertidal, near zero chart datum, July 20, 1974. K. D. Hobson coll. (BCPM 974-259-24, 12 juveniles; the largest mentioned below was destroyed during this study).

Additions to Description: In contrast to the observations by Malmgren (1867), Wollebaek (1912), and McIntosh (1922), the thoracic uncini (Fig. 3A) have posterior handles in adults and juveniles. It is noteworthy that Wollebaek also depicted the specimen from Finmark studied here, which is presumably the holotype (cf. Ditlevsen 1911). The uncini of juveniles (Fig. 3B) differ somewhat from those of adults. The posterior handles are slightly longer and the base is narrower. Also, in frontal view, there are only about 8 large teeth above the rostrum rather than 12–13. The number of rows of the numerous smaller teeth above the large teeth is a little smaller, and hence this section of the seta is not as high as in the adult. Even in the adult, only about 10 uncini were found in the 10th setiger. In the juveniles, the upper and lower thoracic notosetae are bilimbate.

Remarks: Among the moderately well-preserved material from British Columbia, the longest specimen, an anterior fragment with 18 setigers, is about 0.6 cm long. The animals clearly fits the generic diagnosis, being without gills and having 17 thoracic setigers, with uncini found only from the 7th onwards (in double rows from the 9th). In regard to the species identification, a long buccal segment is present, but the skinfold on the posterior edge is not recognizable (cf. Wollebaek 1912, pl. 23, fig. 1). Ventral shields occur through about the 10th setiger. The animals seem to be juveniles because 5–7 posterior thoracic segments are without notosetae as was described by Wilson (1928) for *Loimia medusa* (Savigny). The first abdominal segment can be recognized by having only one row of uncini; the uncini, moreover, are attached to supporting rods.

New record. In the North Pacific, the species was previously known from the seas of Japan and Okhotsk.

Lysilla Malmgren

Lysilla loveni Malmgren

Lysilla loveni Malmgren, 1866:393 — Ushakov 1955: 403 — Hartmann-Schröder 1971:489.

Material: British Columbia: Near Victoria, off Clover Pt., 79 m, Aug. 27, 1976. Personnel of Dobrocky Seatech Ltd. coll., R. O'Clair ident. (Priv. coll., Dobrocky Seatech Ltd., 1 specimen).

Washington: Jamestown, 48°07′51″N, 123°05′11″W, fine sand, 7.5 m, Sept. 2, 1976. C. F. Nyblade coll., R. O'Clair ident. (1 specimen).

Remarks: The animals clearly correspond to the generic diagnosis by being Terebellidae without gills and uncini and with small notopodia. The species is identified by having a highly papillated thoracic region, and six pairs of notopodia. The needlelike setae barely emerge. In the large animal from British Columbia, the six pairs of nephridial papillae are about as large as the notopodia.

Lysilla pacifica Hessle (erroneously recorded from Washington, see under *Polycirrus* sp. I, below) appears to be quite different from *L. loveni*, the type species of the genus: Although also *L. pacifica* lacks uncini, its habitus suggests a *Polycirrus* species (from inspection of the type material in ZMU).

New record (by R. O'Clair). In the North Pacific, the species had been known previously only from the Sea of Japan.

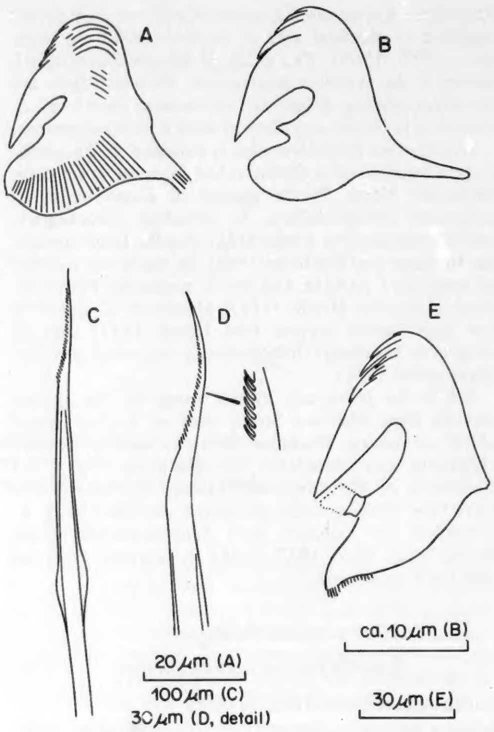

Fig. 3. *Laphania boecki*: A, uncinus from setiger 8; B, uncinus from middle thorax of juvenile (A, holotype; B, BCPM 974-259-24). *Neoamphitrite robusta*: C, long notoseta; D, distal end of short notoseta, with detail of edge; E, uncinus from middle of torus of posterior thorax (C, E, paratype; D, holotype of *Scionides dux*).

Neoamphitrite Hessle

Neoamphitrite robusta (Johnson)
Fig. 3C–E

Amphitrite robusta Johnson, 1901:425 — Hessle 1917: 184.

Terebella robusta — Berkeley 1929:308.

Neoamphitrite robusta — Hartman 1938:17 [under *Amphitrite robusta*]; 1959:511; 1969:605 — Berkeley and Berkeley 1952:85.

Scionides dux Chamberlin, 1919b:266 — Hartman 1938:18; 1959:521; 1969:637.

Material: Washington: Puget Sound, 1898 (MCZ 2398 [previously MCZ 959a], 3 syntypes of *Amphitrite robusta* [partially decayed, dried]).

California: Crescent City, last century (MCZ 2134, holotype, and MCZ 228, 5 paratypes of *Scionides dux*).

— Cape Mendocino, last century R. V. Chamberlin ident. (as *Scionides dux*) (MCZ 75, 6 specimens).

ADDITIONS TO THE DESCRIPTION: Although the type material of *N. robusta* is not well preserved, it can be noted that the six posterior thoracic setigers are without conspicuous ventral shields and that the lower thoracic setae which were not figured by Johnson (1901) have the form shown in Fig. 3C.

The following refers to the type material of *Scionides dux*: The most important observation is that the thoracic notosetae of the specimens, contrary to the explicit statement by Chamberlin (1919b), are distally serrated (Fig. 3C, D). Those of the lower (shorter) series have tips of the characteristic form recognized likewise for the type material of *N. robusta* (see Fig. 3D). Also the form of the uncini from the midparts of middle and posterior thoracic setigers differs from the original description. Most notably, the rostrum is shorter (Fig. 3E) than shown by Chamberlin (1919b, pl. 3, fig. 9); also, the teeth above the rostrum are closely packed, the number in the first series above the main fang being 6 or 7.

The gills are like those figured by Johnson (1901, pl. 16, fig. 164) for *N. robusta.* The segments with gills have weakly developed lateral lappets which are half as wide as the segments are long. The large ventral shields of the anterior and middle thorax become abruptly very small (there is only one transitional segment) so that usually 6 (in 6 specimens; 7 in two, and 8 in one specimen) posterior thoracic setigers have only rudimentary shields in the midventral line. The uncinigerous tori of the anterior abdomen are low and about as long as those of the thorax; posteriorly, they shorten but become slightly elongated and thus form short lappets. The abdominal uncini are arranged in single rows.

The first nephridial papilla was regarded by Chamberlin (1919b) as a nonsetigerous tubercle but it is not nearly as large as a parapodium. Further nephridial papillae are present on setigers 1 through 10 or 11. Glandular tissue not only surrounds the thoracic uncinigerous tori but also both the anteriorly and posteriorly facing bases of the notopodia; this is not the case in material of *N. edwardsi* (Quatrefages) from Washington. Also the nephridial papillae in *S. dux* are surrounded by this tissue (a sexual dimorphism? [cf. Benham 1927]) and therefore are difficult to distinguish except for the two anterior ones, below the second gill and the first notopodium.

REMARK: As the type material of *Scionides dux* agrees fully with *Neoamphitrite robusta* it is considered synonymous with *N. robusta.*

Neoleprea Hessle

REMARK: To evaluate generic diagnostic characters, I reexamined material of *N. californica* which occurs in the southern part of the Oregon Biogeographic Province, and possibly in the northwestern Pacific, in addition to the two species known from British Columbia and Washington. The generic diagnosis by Hessle (1917) is not altered.

Neoleprea californica (Moore)

Terebella (*Schmardanella*) *californica* Moore, 1904: 496 — Hessle 1917:193 — Stasek 1966:14.
Terebella californica — Hartman 1959:523; 1969:643.
not *Terebella californica* — Berkeley and Berkeley 1941:53.
not *Neoleprea californica* — Chlebovitsch 1961:223.

MATERIAL: California: San Diego (CAS 38, holotype; CAS 70, 4 specimens ["virtual paratypes"]).

ADDITIONS TO THE DESCRIPTION: In the type material the first notopodium occurs on the segment with the second pair of gills. Thus, the form has two setigers without uncini and must be included in *Neoleprea* as suggested by Chlebovich (1961). The setae are as described and drawn by Moore (1904). Uncini occur in double rows even in the abdomen, excepting the last 10 or 20 segments (i.e. to at least the 100th segment). Nephridial papillae are present below the first bundle of notosetae (not observed by Moore 1904) and, anterior to and below the notopodia, from the fifth to the 19th–22nd (3 specimens) setiger.

REMARKS: Hessle (1917) pointed out already that Moore (1904) did not express himself clearly regarding the setation and suggested that the species may be a member of *Neoleprea.* Also Hartman (1969) made an error in this regard and, therefore, assigned the species incorrectly to *Terebella.*

The Californian record by Berkeley and Berkeley (1941) belongs to another genus as shown by the thoracic setation described by these authors. For material from the Kurile Islands, Chlebovitsch (1961) has drawn notosetae with terminal sections less bent than is the case with the type material of *N. californicus.* Moreover, he has figured an uncinus with a distinct shoulder behind the small teeth. This is definitely not present in *N. californica* (compare Moore 1904: pl. 38, fig. 37 with Chlebovitch 1961, p. 224, fig. 11b). Finally, the species has been recorded by Buzhinskaja (1967) from the Sea of Japan without providing diagnostic characters. Therefore, the geographic distribution of the species is uncertain.

Neoleprea japonica Hessle

Neoleprea japonica Hessle, 1917:192 — Imajima and Hartman 1964:340.

MATERIAL: British Columbia: Trevor Channel, 48°52.0′N, 125°09.5′W, sand–mud–shell, 27–51 m, April 14, 1975. K. D. Hobson coll. (BCPM 975-167-2, 2 specimens).

Remarks: The two anterior fragments possess 27 and 44 setigers, respectively. They are identified by the following diagnostic characters: two pairs of gills of the form described by Hessle (1917) and 25–26 thoracic setigers of which the first two are without uncini. Uncini occur in double rows from the 7th to the 25th or 26th setigers. The form of the dorsal and ventral setae are as pictured by Hessle (1917). Ventral shields are present on 15 and 17 (the last two very small) setigers, respectively. In both animals, nephridial papillae can be distinguished emerging anterior to and below the notopodia from the 4th to the 15 setiger, and in one they also are distinct on the first setiger.

The two specimens deviate from Hessle's short description by the considerably higher number of nephridial papillae.

New record. The species was previously known only from Japan.

Neoleprea spiralis (Johnson)

Amphitrite spiralis Johnson, 1901:426 — Hessle 1917: 193.
Terebella spiralis — Berkeley 1929:308.
Neoleprea spiralis — Hartman 1938:17 [under *Amphitrite spiralis*]; 1959:511; 1969:607 — Berkeley and Berkeley 1952:84.

Material: British Columbia: Winter Inlet, 54°50′N, 130°27.5′W. In dredge haul over a rock face and into shell and mud, less than 15 m depth, June 10, 1974. P. Lambert coll. (BCPM 974-219-26, 1 specimen). — Massett. E. and C. Berkeley coll., ident. (BCPM 974-543-2, 1 specimen). — Barkley Sound, Bauke I., Sta. 14 N, July 10, 1973. B. Cooke and P. Lambert coll., K. D. Hobson ident. (BCPM 973-166, 1 specimen).

Washington: Near Seattle (MCZ 1874, holotype).

Additions to the Description: The holotype has two thoracic setigers without uncini as already suspected by Hessle (1917) and observed on other specimens by Berkeley and Berkeley (1952). Also, in the holotype, notopodia number 38 (not 41 as stated by Johnson 1901). The specimen was once dried so that the ventral shields and the nephridial papillae are difficult to distinguish. There seem to be 23 or 24 shields of which the last few are small. Papillae can be recognized on one side to the 17th setiger, and on the other side from the 4th to 21st setiger.

The specimens in the British Columbia Provincial Museum have 34, 34, and about 36 notopodia, and 19, 20, and 22 ventral shields, respectively. The uncini are arranged in double rows through setigers 33 or 34. Nephridial papillae occur through the 22nd and 24th or 25th setigers (two specimens) and emerge anterior to and below the notopodia. The openings of the anteriormost nephridia could be recognized only in one specimen (974-543-2) that was well enough preserved: Papillae are present from the 5th (not 4th as in the type) setiger.

All collections from British Columbia are new records which however do not change the known distribution of the species.

Pista Malmgren

Remarks: Material from areas outside the Oregon biogeographical Province was studied to permit clear definition of local species. However, as is the case with *Polycirrus* Grube to be treated below, the genus *Pista* is large and not all members are well known. Because it was not feasible at the present time to reexamine all species, two forms that could not be referred to any known species are briefly described but not named.

Pista brevibranchiata Moore

Fig. 4A

Pista brevibranchiata Moore, 1923:196 — Hartman 1938:18 [under *P. brevibranchia*]; 1959:515; 1969:613.
Pista brevibranchia Chamberlin, 1919b:264 [homonym]. — Hartman 1938:18.
Pista fasciata [not Grube]. — Marenzeller 1884:202 — Berkeley 1929:310 — Berkeley and Berkeley 1952:79 — Imajima and Hartman 1964:343.
Pista fasciata (Grube) *sensu* Marenzeller — Banse and Hobson 1968:45.

Material: Washington: Puget Sound, Sta. 2 and 7 of Lie (1968), mud, 1963. (K. Banse priv. coll., 4 specimens, ident. as *P. fasciata sensu* Marenzeller).

California: Cape Mendocino, last century. A. Agassiz coll. (MCZ 502, holotype of *P. brevibranchia* [in 4 pieces]).

Additions to the Description: The last four or five thoracic setigers are without ventral shields, but a band of glands crosses the ventrum (cf. Banse and Hobson [1968]). A side view of the anterior end (Fig. 4A) complements fig. 1 in Hartman (1969:613). The important, easily recognized diagnostic character is the small lateral folds on segments 6 and 7 as pointed out by Imajima and Hartman (1964) for *P. fasciata sensu* Marenzeller.

Remark: An examination of the material listed herein indicates that the specimens previously identified as *P. fasciata sensu* Marenzeller by Imajima and Hartman (1964) and Banse and Hobson (1968) should be referred to *P. brevibranchiata*, thus adding Japan and Washington to the earlier recorded distribution of western Mexico to California.

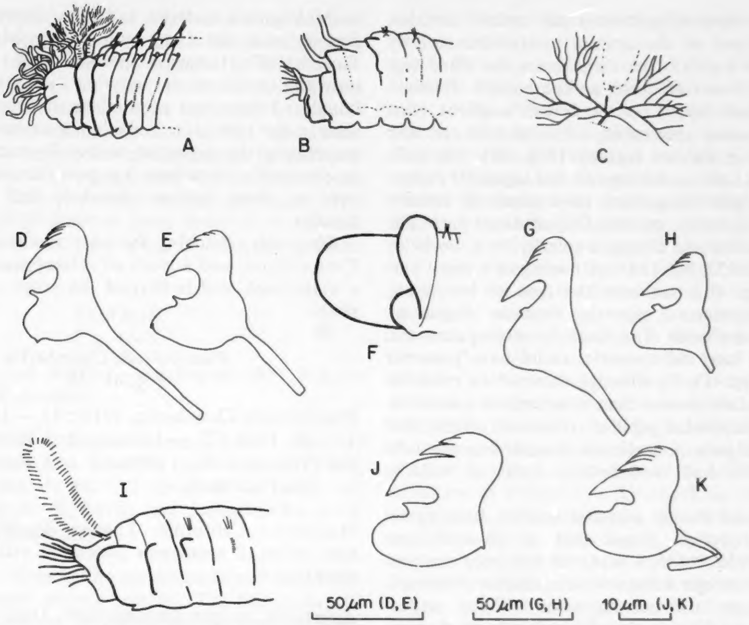

FIG. 4. *Pista brevibranchiata*: A, anterior end from the left [setae schematic] (Washington [drawn by K. D. Hobson]). *Pista cristata*: B, anterior end from the left [setae schematic; tentacles and gills omitted]; C, tracing of gill [at x, a major branch omitted]; D, E, uncini from setigers 2 and 16 (B, SMNH 6674; C–E, SMNH 6675). *Pista fratrella*: F, anterior end from the left [appendages omitted]; G, H, uncini from setigers 4 and 13 (all holotype). *Pista* sp. II (SMNH 6676); I, sketch of anterior end, from the left [tentacles indicated; only large gill shown, presumably incorrectly drawn on segment 1 instead of 2]; J, K, uncini from setigers 2 and 3 (from different animals).

Pista cristata (Müller)

Fig. 4B–E

Amphitrite cristata Müller, 1776:216 (not seen, cited from Hartman 1959:497).

Pista cristata — Malmgren 1866:382 [in part, see Pista sp. II]. — Hessle 1917:154 — Berkeley and Berkeley 1952:78.

MATERIAL: Sweden: Skagerrak coast: Koster I., Ljungman coll. (SMNH 6674, 2 specimens); Väder I., Goës coll. (SMNH 6675, 4 specimens); Bohuslän, Lovén coll. [in part] (SMNH 6677, 3 specimens). All ident. by A. J. Malmgren as *P. cristata*.

British Columbia: Jervis Inlet, 8–20 fms (15–37 m), July 15, 1934. E. and C. Berkeley coll., ident. (USNM 41434, 1 specimen). — Trincomali Channel, 25–30 fms (46–55 m), March 16, 1937. E. and C. Berkeley coll., ident. (USNM 41435, 4 specimens).

Washington: Friday Harbor, 1929. Weese coll., E. and C. Berkeley ident. (USNM 41438, 16 specimens). — San Juan Channel, near Friday Harbor Laboratories, mud with *Modiolus* sp., 40–46 fms (74–84 m), July 15, 1940. M. H. Pettibone coll., ident. (USNM 44436, 2 specimens).

NOTE: Because the figures of Malmgren (1866, pl. 22, fig. 59), Wollebaek (1912, pl. 30, fig. 1), and Ushakov (1955, fig. 144A) are similar to each other but differ greatly from that of Berkeley and Berkeley (1952, fig. 158) and the description by Hessle (1917), the material from the Swedish west coast used by Malmgren for his figures and some of the specimens studied by E. and C. Berkeley were compared. It was found that Malmgren's material contained two species of *Pista* both with 17 thoracic setigers and with gills of the pompon form, typical of *P. cristata*. Neither agrees well with his figure which he himself regarded as poor. One of these appears identical to the one described by Hessle.

In the following, the species is depicted which Hessle (1917) and Berkeley and Berkeley (1952) treated. Only salient features are given. Likewise, the second, similar species of Malmgren's material is briefly described as *Pista* sp. II, without being identified.

Description: Several specimens are mature females. The anterior end of the animal is characterized by lateral lappets (folds); the largest, on the third segment, partly covers the fold on the second. Further, there is a small lappet on the fourth segment (first setiger). On many specimens, a lateral fold can also be recognized on the first segment (Fig. 4B). The gills, usually 2, one each on the 1st and 2nd segments (sometimes 3 or 4 gills altogether) have stems of variable length and a pompon- or oval-shaped distal part. The terminal branches are arranged spirally (e.g. Berkeley and Berkeley 1952, fig. 158). A tracing of a small part of a gill (Fig. 4C) indicates the type of branching. Usually 3, sometimes 2, posterior thoracic setigers are without ventral shields. The thoracic uncinigerous tori are relatively long. All thoracic uncini have posterior extensions (Fig. 4D, E) although those of the posterior thoracic uncini are shorter than those present anteriorly. Conspicuous nephridial papillae are present on the third and fourth setigers. A specimen preserved in the tube (SMNH 6675) had used broken shells as building material.

The northeast Pacific material studied here agrees with this description except that of 20 specimens checked (USNM 41435, 41438) 18 had only one posterior thoracic setiger without ventral shields (one each, all setigers with, and two segments without, respectively). Also, in large, especially well-preserved specimens (USNM 44436), the lateral fold on the first segment is definitely absent. One sample (USNM 41436) contains animals in a thick tube of fine sand while usually, *P. cristata* is reported as having a tube with heavy mud walls.

Remarks: Although it turned out that Malmgren (1866) had two species before him, it is clear that most if not all of his description refers to what has been called here *Pista cristata*. Especially relevant is his observation of posterior handles on the uncini in the (anterior) setigers which he incorporated in the generic diagnosis of *Pista*. These handles are very difficult to make out in *Pista* sp. II (see below).

Pista cristata has been reported from so many localities that it might be regarded as having a worldwide distribution. Pending a thorough revision, it is not clear, however, whether all these records are correct. Even those from the boreal region that have been well described differ, for instance, in regard to the form and occurrence of the lateral folds and the occurrence of uncini with posterior elongations. For example, Wollebaek (1912, pl. 30, fig. 1) did not show a fold on the second setiger and drew gills definitely different from those in Malmgren's material; Ushakov (1955, fig. 144A) did not show folds on the second, and the fourth segments, and drew very short thoracic uncinigerous tori. On the other hand, Berkeley and Berkeley (1952, fig. 158) depicted a large fold on the fourth segment which is absent in their specimens. Elsewhere, Day (1967, fig. 36.7h) drew folds as seen in Malmgren's material and also showed one on the first segment; like many authors (e.g. Malmgren 1866; Fauvel 1927; Hartmann-Schröder 1971) he stated that only the uncini of the anterior thorax have posterior handles. I note that these elongations can usually be seen in the tori with double rows of uncini only after macerating the dissected series of setae mechanically or chemically; therefore, it is possible that the methods used by those authors failed to find the posterior handles.

Obviously, checking the very numerous records of *Pista cristata*, and a study of related species, would be a major task and is beyond the scope of the present study.

Pista fratrella Chamberlin

Fig. 4F–H

Pista fratrella Chamberlin, 1919c:18 — Hartman 1938: 18; 1969:623 — Berkeley and Berkeley 1941:53.
not *Pista fratrella* — Berkeley and Berkeley 1952:80 [see *Pista* sp. I].

Material: California: Laguna Beach (MCZ 2168, type series, 2 specimens [dried] in vial, 1 slide with setae).

Additions to the Description: Only one specimen, which apparently is the holotype, permits any useful observations. In side view (Fig. 4F) the lateral lappets on segment 1 (peristomium in Chamberlin 1919c) hide the anterior parts of the animal completely. The large lappets on the third segment rise laterally above the dorsum, but the connection across the dorsum mentioned by Chamberlin must be quite low. Importantly, Chamberlin failed to observe a pair of lower, small lappets on what appears, in the dried material, to be the second segment. The lappets on the fourth segment originally described cannot be seen any more. The last four or five thoracic setigers are without ventral shields. Anterior thoracic uncini are shown in Fig. 4G; the posterior uncini have much reduced posterior elongations (Fig. 4H).

Remark: Hartman (1969:624) remarked that the species "bears resemblance to *Pista fasciata*, insofar as known." As the only other material identified as *P. fratrella* is also poorly preserved (Berkeley and Berkeley 1941), the species remains incompletely known. New collections are needed to fully describe the species.

Pista sp. I

Pista fratrella [not Chamberlin]. — Berkeley and Berkeley 1952:80.

Material: British Columbia: Off Cape Cook, deep water, April 18, 1929. E. and C. Berkeley coll., ident. as *P. fratrella* (USNM 41431, 1 specimen).

DESCRIPTION: The animal is small and some features are difficult to see, but apparently large lateral lappets insert on the third segment (similar to those in *P. fratrella*, cf. Fig. 4F) in a ventro-lateral position and also on the second segment. The large fold or lappets covering the prostomium in that species are absent here. Thus, the description of the lappets by Berkeley and Berkeley (1952) paraphrases that by Chamberlin (1919c) but does not refer to this specimen. The uncini are slightly different from those of *P. fratrella* in the outline of the basal part, beneath the rostrum (around the guard).

Pista sp. II
Fig. 4I–K

Pista cristata [not Müller] — Malmgren 1866:382 [in part, see *P. cristata*].

MATERIAL: Sweden: Skagerrak coast, Lind I. (SMNH 6676, 7 specimens). — Bohuslän (now in SMNH 6676, originally in SMNH 6677; 1 specimen, in tube). All were collected by S. Lovén and identified by A. J. Malmgren as *Pista cristata*.

DESCRIPTION: None of the specimens is well preserved. There are several mature females. The thorax has 17 setigers of which one to four of the last ones are without ventral shields. The gills, usually two (in some, three) are of greatly unequal size, the largest (Fig. 4I) being longer than those of *P. cristata*. Macroscopically, the terminal branches are not arranged obviously in spirals. The actual branching is similar to that of *P. cristata*. Lateral folds are present on segments 2 to 4, the largest being on segment 2 (Fig. 4I). The thoracic uncinigerous tori are short (cf. Fig. 4I and 4B). Even on the second and third setigers, the uncini have only very slender posterior elongations (Fig. 4K) which are much finer than, for example, the supporting rods in the abdominal tori in the Polycirrinae. In some preparations of anterior parapodia, I was unable to see them (e.g. Fig. 4J) and have failed to find posterior elongations in any of the posterior thoracic notopodia examined. Similarly, posterior elongations seem to be missing in anterior setigers in other species assigned to *Pista* (e.g. Day 1967:736; also remarks on *Axionice*, under *Betapista*, herein). Nephridial papillae could not be recognized on any of the specimens, possibly owing to the poor state of preservation. One specimen was surrounded by a mud tube.

This species of *Pista* is not one of those known from northern Europe (cf. Wollebaek 1912 [under *Scione*]; Hartmann-Schröder 1971).

Polycirrus Grube

REMARKS: The following species of *Polycirrus* have been recorded previously from the continental shelves of the temperate North Pacific Ocean, between the area north of Tokyo Bay and the Pacific coast of Lower (Baja) California (see records or reviews in Rioja 1947; Berkeley and Berkeley 1952; Pettibone 1954; Ushakov 1955; Imajima and Hartman 1964; and Hartman 1969): *P. caliendrum* Claparède; *P. californicus* Moore; *P. eous* Annenkova; the junior homonym of *P. kerguelensis* McIntosh; *P. medusa* Grube; *P. mexicanus* (Rioja); and *P. perplexus* Moore. Further, *P. medius* Hessle and *P. nervosus* Marenzeller occur in Sagami Bay, south of Tokyo Bay.

Below it will be shown that *P. perplexus* is a synonym of *P. californicus* and that the North Pacific records for *P. caliendrum* and the homonym of *P. kerguelensis* are apparently incorrect, as is also the record for *P. medusa* from the Northeast Pacific. On the other hand, in addition to *P. californicus*, five species have been found in British Columbia and Washington waters that cannot be named and which seem to be neither of the above; admittedly, however, *P. eous* is not fully known (cf. the original description of the setae by Annenkova 1924 with that in Ushakov 1955, under the generic definition of *Polycirrus*). To check on other published descriptions, I inspected the type series of *P. medius* and *P. nervosus* from Japan, and specimens of *P. medusa* from the Swedish west coast (all in ZMU). For all, the descriptions were substantiated.

The five unknown species of *Polycirrus* are not named, for the following reason: The present study is entirely motivated by the wish to complete the organization of the existing faunistic knowledge of the benthic polychaetes in the northern part of the Oregon Province, which was initiated by the late K. D. Hobson, before her contribution becomes outdated. To name five new species (if they are new) would require the consideration of the entire genus. A perusal of some of the description of the species regarded as valid (cf. Hartman 1959), however, showed that the task amounts to a revision of a very difficult genus. The situation at the present time seems to remain as stated by Hartman (1969:629): "As currently known, the genus is confused, the specific characters are so variable that distinction [of species from California] is not possible." Possibly, not all diagnostic characters are variable but, certainly, they are poorly known. Thus, the five unidentified species are briefly described below to permit recognition at a later date and to contribute to the knowledge of the genus. Principal characters used are the number of notopodia (only gross differences being of diagnostic value) and the first segment of their occurrence; the arrangement and approximate number of ventral (lateral) pads; the form of the notopodia; the form of the notosetae and uncini; and the number of nephridia. In contrast to most previous authors, the frontal view of the uncini that often yields conspicuous differences among species is emphasized.

The following key utilizes only the gross number of notopodia, the presence or absence of dorsal cirri, and the form of notosetae and uncini. Noting that all species in the key have only six nephridia, the key is applicable in the entire temperate North Pacific, with the provision that *P. eous* (with 20 thoracic segments) and *P. mexicanus* (with plumose notosetae) are not differentiated.

1 Notosetae plumose (Fig. 6E), sometimes also limbate. With 10–14 [rarely 15] pairs of notopodia .... *Polycirrus* sp. I
Notopodia limbate [smooth under low magnification, variously ornamented under oil lens] 2

2 With 10–15 pairs of notopodia 3
With 20–25 [40] pairs of notopodia 5

3 Notosetae weakly serrate (Fig. 7E). Uncinus with semicircle of large teeth above secondary tooth (Fig. 7G) .... *Polycirrus* sp. III
Notosetae with fine hairs (as in Fig. 7B) 4

4 Uncinus with 0 to 3 smaller teeth above secondary tooth (Fig. 7D) .... *Polycirrus* sp. II
Uncinus with numerous small teeth above and to side of secondary tooth (Fig. 8I) . . *Polycirrus* sp. V

5 Notopodia usually with conspicuous posterior lips (Fig. 5C, D). Uncinus with semicircle of small teeth above secondary tooth (Fig. 5I) .... *P. californicus* Moore
Notopodia without conspicuous posterior lips. Uncinus without teeth above 1 or 2 small teeth above principal tooth (Fig. 8D) . . *Polycirrus* sp. IV

Polycirrus californicus Moore
Fig. 5

Polycirrus californicus Moore, 1909:276 — Hartman 1959:517; 1969:629.
Polycirrus perplexus Moore, 1923:198 — Berkeley 1929:310 — Weese 1932:21 — Hartman 1959: 518; 1969:631.
Polycirrus caliendrum [not Claparède] — Berkeley and Berkeley 1942:204; 1952:77.

MATERIAL: British Columbia: Banks I., Bayon, 58°37.7′N, 130°0′W, rocky intertidal, near zero chart datum, July 20, 1974. K. D. Hobson coll., ident. as *P. kerguelensis* (BCPM 974-258-49, 2 specimens). — Victoria: Smuggler's Cove, intertidal, April 23, 1974. K. D. Hobson coll. (?), ident. as *P. caliendrum* (BCPM 974-83-3, 2 specimens); shell–gravel on rock island, intertidal, May 21, 1974. K. D. Hobson coll., ident. as *P. caliendrum* (BCPM 974-123-7, 1 mature and 2 juvenile specimens [questionable identification by K. B. for the latter]). — Barkley Sound: Bauke I., Sta. 36N, July 11, 1973. B. Cooke and P. Lambert coll., K. D. Hobson ident. as *P. caliendrum* (BCPM 973-168, 4 specimens, some mature); Erin I., 48°55.5′N, 125°15.7′W [from chart; not on label], solid rock outcropping from sand and gravel, Aug. 7, 1973. B. Cooke and P. Lambert coll. (?), K. D. Hobson ident. as *P. caliendrum* (BCPM 973-194-53, 1 specimen).

Washington: Harney Pass, about 48°35.5′N, 122°55′W, mud, 15 fms (27 m), July 1967. H. L. Sanders coll. (K. Banse, priv. coll., 1 specimen). — Jamestown, 48°07′51″N, 123°05′11″W, fine sand, 7.5 m, Sept. 2, 1976. C. F. Nyblade coll. (12 specimens).

California: Monterey Bay [from label] 48–111 fms (88–203 m), 1904 (USNM 17366, holotype of *P. perplexus*). — Off Gull I. [so. coast of Santa Cruz I.], Albatross Sta. 4430, 197–281 fms (360–514 m), April 14, 1904, J. P. Moore ident. as *P. perplexus* (USNM 17365, 1 specimen). — San Diego, Dec. 1902 (CAS 005272, holotype of *P. californicus*).

ADDITION TO THE DESCRIPTION: First, additions and corrections to the descriptions of the holotypes of *P. californicus* and *P. perplexus* (both from California) will be reported before the material from British Columbia is presented. This is followed by a discussion of the synonymy.

The anterior end of the holotype of *P. californicus* is sketched in Fig. 5A (see also Fig. 5B). The ventral sides of parapodia 4–6 are thickened suggesting the location of the nephridial openings (papillae were not visible). Therefore it seems certain that the first setiger is segment 3 and not segment 2 as stated by Moore (1909). The notopodia possess conspicuous posterior lips (as in Fig. 5C, D). Another important observation is that the first uncini occur on setiger 8 rather than 13 as stated by Moore (1909). The thoracic and abdominal uncini are essentially alike (dissected on setigers 8, about 32, and far posteriorly). They possess a semicircle of small teeth above a large secondary tooth (as in Fig. 5G–I). Notosetae are not simply limbate as stated by Moore (1909) but have hairs that, viewed with an oil immersion lens, are especially conspicuous in the distal sections of setae, both those of the long and short series (as in Fig. 5E, F).

As stated by Moore (1923), the holotype of *P. perplexus* is 5.4 cm long and has 40 segments with notosetae. Figure 5B illustrates the description by Moore (1923) of the ventral view of the anterior end. The dorsum of the thorax is clearly segmented. Posterior notopodial lips (Fig. 5C) are present throughout. The notosetae are similar to Fig. 5E. Those of the smaller series are beset with hairs from approximately the middle of their widened sections (Fig. 5F). Conspicuous uncinigerous tori, approximately earshaped, start on setiger 8 (segment 10, from position of nephridial papillae). The thoracic and abdominal tori lend the specimen a habitus somewhat different from that of the other material studied here. Uncini of anterior and posterior segments (dissected on setigers 9, 14 and far posteriorly) are alike (Fig. 5G). Setigers 1 through 6 bear nephridial papillae, the anterior three being smaller than the posterior three; Moore (1923) seems to have referred to these papillae when describing tori in the first setigers. There is neither a papilla nor

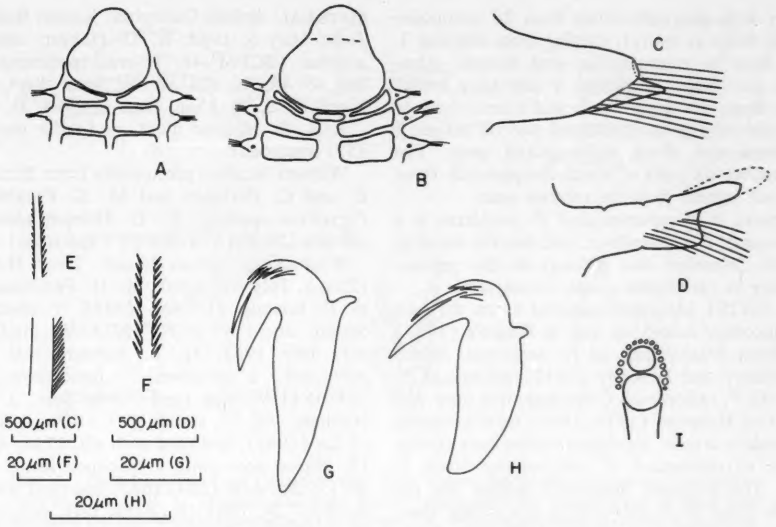

FIG. 5. *Polycirrus californicus*: A, B, anterior end from below [schematic]; C, notopodium 5, anterior view; D, in situ posterior notopodium from above [dotted outline, extended posterior lip]; E, middle and distal section of notoseta; F, distal section of notoseta; G, H, uncini from middle abdomen, side view [striation omitted]; I, head of uncinus in middle abdomen, frontal view [schematic] (A, holotype; B, C, F, G, holotype of *P. perplexus*; D, E, H, I, British Columbia).

a torus on setiger 7. The left notopodium of setiger 2 is malformed (Fig. 5B).

The new material from British Columbia is quite similar in appearance to the holotype of *P. californicus*. From the observations of this larger material, the following may be noted: While the holotypes of *P. californicus* (a mature female) and *P. perplexus* are 2.8 and 5.4 cm long and have 28 and 40 pairs of notopodia, respectively (from Moore 1909; 1923), a large, complete specimen from British Columbia measures 4.5 cm and has about 80 segments in all. Other animals are of about the same size. They possess usually 24 or 25 segments with notosetae (one mature male, 18; one specimen, 19; one, 21); few seem to be mature. The anterior end usually bears a huge mass of tentacles of two kinds in which much of the thoracic region can be hidden. Viewed from the dorsum one annulus precedes the first setiger (segment 3) but the rest of the dorsum is only faintly segmented. Ventrally, a rhomboid pad is formed by segments 1 and 2 while segment 3 bears a pair of reduced pads (as in Fig. 5A but connected midventrally). The next six to eight setigers (nine in a very large animal from Friday Harbor) possess large pairs of tumid pads which meet in the midventral line. Several following setigers have small lateral pads.

Notopodia are long and have a distinct cirrus (the elongated posterior lip), especially in the posterior thorax (Fig. 5D). These are ordinarily quite conspicuous in entire animals, before dissection. Notosetae appear to be limbate; however, under an oil immersion lens, the "wing" of the series of large setae (distal to its widest section), consists of fine spines that separate in a bent seta; in the series of smaller setae, the spines are less closely spaced and appear as hairs (Fig. 5E). Uncini start on the 8th to 13th setigers, with smaller animals apparently having the lower beginning number. In the abdomen, the uncini are placed on small, nearly circular lappets which are directed posteriorly and give a very distinct segmentation to the ventral side. These lappets are even more distinct in the holotype of *P. perplexus* but less so in *P. californicus* from British Columbia. The midthoracic and abdominal uncini have essentially the same outline (Fig. 5H). A long tooth above the rostrum is conspicuous, above which is a semicircle of small teeth (Fig. 5I).

The three anterior nephridia each extend through about three segments while the three posterior ones are restricted to one segment each (from dissection, BCPM 974-83-3). In some animals, the three posterior pairs possess large external papillae beneath the notopodia. The color of the preserved material is greenish or yellowish-white. The gut content is fine material, with a few grains of fine sand (BCPM 974-83-3).

REMARKS: *Polycirrus californicus* can be characterized as a species with generally more than 20 notopodia (occasionally twice as many), starting from segment 3. Notopodia have a postsetal lip and hirsute setae. Neuropodia may begin on setiger 8 and have uncini each with a large secondary tooth and a semicircle of small teeth above. The ventro-lateral pad on setiger 1 is small; there are about eight paired pads. The nephridia number six pairs of which the posterior three pairs are much smaller than the anterior ones.

On this basis, it is apparent that *P. perplexus* is a junior synonym of *P. californicus*, and that the material from British Columbia also belongs to the species, thus extending its geographic range considerably.

Berkeley (1929) identified material from the east coast of Vancouver Island, as well as Weese's (1932) specimens from Washington, as *P. perplexus*. Subsequently, Berkeley and Berkeley (1942) synomized *P. perplexus* with *P. caliendrum* Claparède; this view was not accepted by Hartman (1959; 1969) who, however, did not provide a reason. New observation here clearly permits one to distinguish *P. californicus* from *P. caliendrum*. The principal diagnostic feature are the uncini: while those of *P. californicus* are of one kind, the thoracic and abdominal uncini in *P. caliendrum*, described and depicted by Saint-Joseph (1894) and Soulier (1904), differ from each other. Further, the pictures of the uncini of *P. caliendrum* by these latter two authors show that both used oil-immersion lenses while studying their animals; yet, they state that the thoracic notosetae are limbate or smooth; I presume, therefore, that the notosetae were in fact smooth while those of *P. californicus* are not.

Berkeley and Berkeley (1952) listed three localities for *P. caliendrum*: East coast of Vancouver I., Departure Bay, 10 fms (see Berkeley 1929 [as *P. perplexus*]): West coast of Vancouver I., littoral; and Friday Harbor, Washington. No sample is preserved from the first named site. The second record is a misidentification: The undated sample of the Berkeley material in the USNM (No. 41229) is a fragment of a (presumably juvenile) species without gills, of the Amphitritinae. The last locality is presumably the record of *P. perplexus* by Weese (1932; identified by E. Berkeley). Because of the lost specimens it can only be surmised that *P. caliendrum* is not a member of the fauna of British Columbia and Washington; hence, the species is likely to be absent from the North Pacific Ocean.

Polycirrus californicus has not previously been recognized in British Columbia or Washington waters.

Polycirrus sp. I
Fig. 6

Polycirrus sp. I. Lie, 1968:287 — Banse et al. 1968: 547.

Lysilla pacifica [not Hessle] — Banse and Nichols 1968:226 — Banse et al. 1968:546 — Lie 1968: 296.

MATERIAL: British Columbia: Kanish Bay, sandy mud, 38 m, May 5, 1965. K. D. Hobson ident. as *Lysilla pacifica* (BCPM 41, several specimens). — Blubber Bay, 49°48.2′N, 124°37.1′W [from chart, not on label], clayey sand, 25–35 m, Dec. 8, 1965. D. V. Ellis coll. (?), K. D. Hobson ident. as *Lysilla pacifica* (BCPM 45, 1 specimen).

Without locality; presumably from British Columbia. E. and C. Berkeley and M. H. Pettibone ident. as *Polycirrus medusa*; K. D. Hobson ident. as *Lysilla pacifica* (BCPM 974-284-25, 1 specimen).

Washington: Orcas Island: Deer Harbor, 12 fms (22 m), July 12, 1940. M. H. Pettibone coll., ident. as *P. medusa* (USNM 44486, 1 specimen); West Sound, about 48°36′N, 122°57′W, mud, 22 fms (40 m), July 1957. H. L. Sanders coll. (K. Banse, priv. coll., 1 specimen). — Jamestown, 48°07′51″N, 123°05′11″W, fine sand 7.5 m, Sept. 2, 1976. C. F. Nyblade coll. (3 specimens). — Puget Sound: Sta. 3 of Lie (1968), fine sand with silt, 17 m, April 29, 1963 (K. Banse priv. coll., 1 specimen ident. as *Polycirrus* sp. I); Sta. 4 of Lie (1968), fine sand with silt, 10–12 m, April 29, 1963 (K. Banse priv. coll., several specimens, ident. as *Lysilla pacifica*).

DESCRIPTION: One of the large individuals, of about 3.5 cm length, possesses about 100 segments. Usually, 10 segments bear notopodia (2 Washington specimens; 5 from British Columbia had 10 and 1 had 11 pairs of notopodia). However, a small animal of about 1 cm length (without the numerous tentacles) had 14 notopodia (see Hessle 1917 for similar observations on variability in *P. medius*). The tentacular membrane which is very large has 4 to 6 undulations. The thoracic segments are dorsally biannulate and not as markedly inflated as in most *Polycirrus* species (Fig. 6A). The thoracic epidermis is nearly smooth under low magnification. Ventrally (Fig. 6B) segment 1 forms the anterior pad; behind (on segment 2) is a narrow pad that seems to transverse the entire ventrum. Under different contraction of the animals, it may be partially covered by the anterior pad (Fig. 6C). The paired pads of segments 3–7 (segment 3 being the first setiger) are usually distinct, rectangular and unusually broad so that only a narrow midventral area is left free; there may be rudimentary pairs on the following 2 segments. Thereafter, some glandular tissue is present which does not form distinct pads.

The unusually long notopodia (Fig. 6A) are broad and fan-shaped in anterior view (Fig. 6D) and possess a cirrus-like, short dorsal extension. The notosetae are usually plumose; close inspection of broken tips reveals closely stacked cones (Fig. 6E) which separate fully in bent setae. A few notosetae may be limbate. Neuropodial lobes are absent throughout. Uncini are missing in the thoracic setigers but start on one of the next few segments [one speciment dissected]. Generally, they are difficult to find, sometimes even upon dissec-

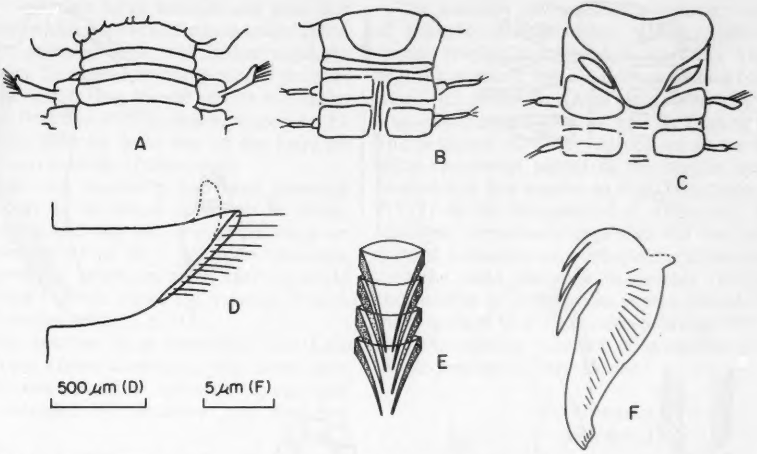

FIG. 6. *Polycirrus* sp. I: A, anterior end from above [parapodia schematic; tentacular lobe indicated]; B, C, anterior end from below [schematic]; D, notopodium [broken line indicates the occasional appearance of a "cirrus"]; E, detail of plumose notoseta; F, uncinus from middle abdomen, side view (Washington; A, USNM 44486).

tion, unless the epidermis is transparent or the tori are elevated as sometimes in the middle abdomen. The shape of the uncini is the same in the anterior and middle abdomen (Fig. 6F). Apparently, two teeth sit above the main tooth, and the vertex is formed by three teeth. The number of uncini per torus is about 10 (anteriorly) to 20 to 25 (midabdomen). There are six pairs of nephridia, the last in the 6th setiger. The first three, especially the third, are much larger than the second three. External papillae were not found. The color of the preserved material is usually dark brown or red.

REMARKS: *Polycirrus* sp. I resembles *P. mexicanus* (Rioja) from Baja California (Rioja 1947) in having the same kind of notopodial cirri and two types of notosetae. *Polycirrus mexicanus* has a greater number (14–18) of thoracic segments (with some overlap, however) and the uncini seem to be different. The number of nephridia was not noted by Rioja. Plumose setae are known in four other *Polycirrus* species (see Day 1973, under *P. carolinensis* Day), but they all differ from *Polycirrus* sp. I in several other characters, such as the starting segment bearing setae, or grossly different number of segments with notosetae, or the number of nephridia.

Polycirrus sp. I differs from *P. medusa* Grube by *inter alia* the possession of plumose setae. My failure to find the uncini is the reason for assigning the species to *Lysilla pacifica* Hessle in Banse and Nichols (1968); the same seems to have happened to K. D. Hobson.

Polycirrus sp. II
Fig. 7A–D

Polycirrus medusa [not Grube] — Pettibone 1954:328 — Berkeley 1968:563.

MATERIAL: Washington: San Juan Archipelago: Off Henry I., Aug. 10, 1938 (USNM 44485, 1 specimen); Washington Channel, near Friday Harbor Laboratories, San Juan I., mud with *Modiolus*, 40–46 fms (73–84 m), July 15, 1940 (USNM 44487, 4 specimens); Lopez I., off Flat Point, July 15, 1938 (USNM 44484, 1 specimen). All collected by M. H. Pettibone and identified as *P. medusa.*

DESCRIPTION: All specimens, including some mature, are incomplete but well preserved. There are 13 segments with notosetae and at least 20 abdominal segments (presumably far more than this number). The fragment with 20 abdominal segments is almost 3 cm long. The anterior end bears a large, trilobate tentacular membrane. The thoracic segments are dorsally faintly biannulate and divided by longitudinal folds into many small fields which make the epidermis appear almost papillose. Ventrally, segments 1 and 2 (the first setigerous segment) form a central large pad (Fig. 7A). Segment 3 possesses a pair of triangular lateral pads. Approximately rectangular, large pads occur on about six following segments. Thereafter, the pads are greatly reduced.

Notopodia in anterior view are about twice as long as they are wide and have small lips; posteriorly, a

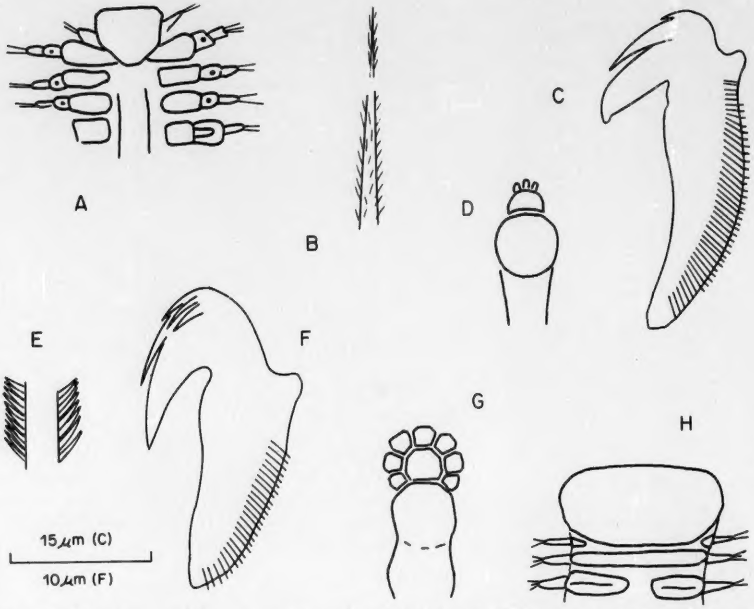

FIG. 7. *Polycirrus* sp. II: A, anterior end from below [schematic]; B, middle and distal parts of notoseta; C, anterior uncinus, side view; D, head of anterior uncinus, frontal view. *Polycirrus* sp. III: E, middle part of notoseta; F, anterior uncinus, side view; G, head of anterior uncinus, frontal view. *Ereutho kerguelensis*: H, anterior end from below [schematic] (smaller syntype).

small, knob-like dorsal cirrus may be present. From setiger 2 through 7 nephridial papillae are visible in the mature animals; in setigers 5–7, they are surrounded by large, sucker-like pads; also dissection showed the presence of six pairs of nephridia. Notosetae appear under low magnification only weakly limbate, almost capillary. Under high magnification, numerous fine hairs can be seen in their middle and distal parts (Fig. 7B). Neuropodia begin on the segment following the last setiger with notopodia. Tori are about as long as they are wide. Most uncini in the anterior and posterior abdomen have only a single tooth above the rostrum, but sometimes two or three tiny teeth, side by side above the secondary tooth are present (Fig. 7C, D).

REMARKS: *Polycirrus* sp. II may be distinguished from *Polycirrus medusa* by *inter alia* the central ventral pad formed by the first two segments, rather than three, and the beginning of notosetae on segment 2 rather than 3 (see Hessle 1917; Fauvel 1923; Hartmann-Schröder 1971). The former two authors also describe uncini for *P. medusa* that are different from those depicted in Fig. 7C. There are no valid records of *P. medusa* from the Northeast Pacific because other Washington and British Columbia records of the species have been referred herein to *Polycirrus* sp. I. *P. medusa* has been reported from the Northwest Pacific by several authors, e.g. Ushakov (1955).

Polycirrus sp. III
Fig. 7E–G

Polycirrus kerguelensis [not McIntosh] — Berkeley and Berkeley 1942:204; 1952:78.

MATERIAL: British Columbia: west coast of Vancouver Island. E. and C. Berkeley coll., ident. as *P. kerguelensis* (USNM 41228, 1 specimen).

DESCRIPTION: The large, apparently complete animal is moderately well preserved. It has 12 segments with notosetae and about 45 abdominal segments. The anterior end cannot be fully described. The tentacular membrane is trilobed and convoluted. The thoracic segments are clearly segmented, with two annuli per segment which in turn are subdivided by longitudinal folds so that the epidermis is coarsely rugose. The last five thoracic segments are without lateral pads. Notopodia start on segment 3 (determined from the location of the nephridial papillae on setigers 4–6, cf. Hessle 1917:222), are about twice as long as wide (anterior view), and have large anterior and posterior lips. The notosetae which appear as limbate under 200× magnification are actually beset with rather regularly arranged fine hairs. In optical section under high magnification (Fig. 7E), they may appear serrate (so called by Berkeley and Berkeley 1952); this arrangement of the setae is clearly different from that of the hairs on the setae of e.g. *Polycirrus* sp. I (see above).

Because the last two notopodia had been dissected previously, the start of the uncini could not be determined. In the abdomen, the tori are about twice as long (dorsally–ventrally) as they are wide. Anterior (Fig. 7F) and posterior uncini are alike; a strong single (very rarely double) tooth above the rostrum is surmounted by 6–8 smaller teeth (Fig. 7G).

There are three anterior, large nephridia, and three posterior small ones (from dissection); the latter open through conspicuous papillae below the enlarged notopodia, as recorded by Berkeley and Berkeley (1952).

REMARKS: The specimen considered here is assumed to be the one referred to *Polycirrus kerguelensis* (McIntosh) by Berkeley and Berkeley (1942) [the label is not written by them and the date is missing]. McIntosh (1885) described the new species *Ereutho kerguelensis* and *Polycirrus kerguelensis*. Subsequently, *Ereutho* was placed in synonymy with *Polycirrus* so that *E. kerguelensis*, if a valid species (see below), is a secondary homonym of *P. kerguelensis*. Berkeley and Berkeley (1942) placed *E. kerguelensis* in synonymy with *Polycirrus kerguelensis* although they recognized that *P. kerguelensis* McIntosh could be distinguished. Other authors, e.g. Hessle (1917) and Hartman (1966), however, believed that McIntosh's material was of the same species.

I have examined the syntypes of *E. kerguelensis* McIntosh, 1885 (BM 1885:12:1:371) as well as the holotype of *Polycirrus kerguelensis* McIntosh, 1885 (BM 1885:12:1:372). The former sample contains a dissected posterior thorax (segments 5 onwards), a large abdomen — presumably of the same specimen — and a complete, smaller individual. The holotype of *P. kerguelensis* is a badly macerated (from dissection) anterior (essentially, only the thorax) fragment of a juvenile specimen. The anterior setation of the smaller syntype of *E. kerguelensis* is sketched in Fig. 7H; the specimen agrees with McIntosh's description which seems to refer mainly to the larger specimen as far as the thorax is concerned; thus, the notopodia start on segment 2. The notopodia on the holotype of *P. kerguelensis*, however, clearly start on the next segment. Hence, I agree with E. and C. Berkeley (1942) that McIntosh (1885) had two species before him. Therefore, the species described as *Ereutho kerguelensis* is a junior secondary homonym of *Polycirrus kerguelensis* and a replacement name is required — a duty best undertaken by the first reviser of the genus. It is unfortunate that the holotype of *P. kerguelensis* is so poorly preserved as McIntosh's description was incomplete. *Polycirrus kerguelensis* McIntosh, therefore, must be regarded at present as unidentifiable.

The specimen discussed here, contrary to the opinion of Berkeley and Berkeley (1942), differs from the species originally referred to *Ereutho*. The notosetae begin on segment 3 rather than segment 2 (see Fig. 7H). Also, the thoracic dorsal epidermis has a different appearance under low as well as high magnification. The notosetae, however, agreee, as do the uncini [posterior abdominal uncini of the smaller syntype of *E. kerguelensis* are similar to Fig. 7F]. Note that Hessle (1917) in his diagnosis of *P.* (*Ereutho*) *kerguelensis* McIntosh apparently regarded the variability in the start of notosetae as a subspecific character, while he used the same character in another subfamily of the Terebellidae to differentiate genera (Hessle 1917:150). Other authors (e.g. Hartmann-Schröder 1971:486) employ the starting segment of notosetae to distinguish species among the Polycirrinae.

Polycirrus sp. IV

Fig. 8A–D

MATERIAL: Washington: Massacre Bay, Orcas I.: about 48°38.0′N, 122°59′W, mud, 14 m (8 fms), July 1967. H. L. Sanders coll. (BCPM 978-179-1, 10+ specimens).

DESCRIPTION: Most of the specimens are juveniles; the few large ones are broken except a mature female with about 75 setigers that is about 3 cm long. The number of setigers with notosetae is 20–22 in large animals. The anterior end bears tentacles apparently of only one kind, inserting on a thoracic membrane undulating in about five waves. Eyes are absent. All segments are biannulate. The epidermis which appears smooth under low magnification is weakly divided into small rectangles in the thorax. Seen from the dorsal side, one annulus precedes the first setiger (segment 3, determined from dissection). Ventrally (Fig. 8A) a trapezoidal pad seems to be formed by segments 1 and 2; the pad of segment 3 appears to be continuous across the ventrum while the following ones are divided. The midventral area is unusually glandular in the anterior thorax (cf. Fig. 8A). The last pair of pads is found on setiger 5, but there is a small rudimentary pad-like region on setiger 6.

Notopodia are long and possess a large lip above the setae (Fig. 8B). Notopodia 2–6 are somewhat longer than the remaining ones. Notosetae are narrowly limbate; under an oil immersion lens, the "wings" are almost smooth with only the edges fringed with hair-like fibers. Neuropodia, except ooccasionally when colored, are scarcely visible so their beginning could not be determined. The uncini are each characterized by 1 (occasionally 2) large tooth above the rostrum (Fig. 8C, D), without accessory teeth above.

The three anterior nephridia (in setigers 1–3) extend through two to three segments; the three posterior ones in the three following segments are smaller. External papillae are absent. The egg diameter is about 70 μm. The color of the preserved material is pink.

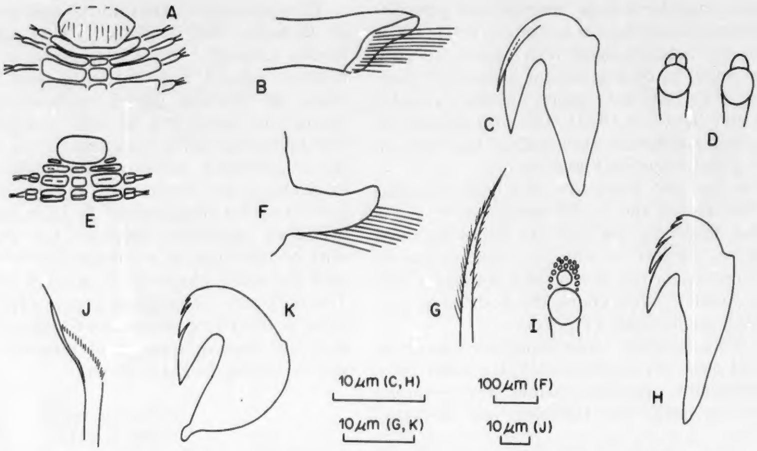

FIG. 8. *Polycirrus* sp. IV: A, anterior end from below [schematic]; B, notopodium [setae schematic]; C, uncinus, side view; D, heads of two uncini, frontal view [schematic]. *Polycirrus* sp. V: E, anterior end from below [schematic]; F, notopodium (setae schematic); G, tip of notosetae; H, uncinus, side view; I, head of uncinus, frontal view [schematic]. *Scionides reticulata*: J, notoseta from middle thorax; K, uncinus (both holotype).

Polycirrus sp. V
Fig. 8E–I

MATERIAL: Washington: Jamestown, 48°07′51″N, 123°05′11″W, fine sand, 7.5 m, Sept. 2, 1976. C. F. Nyblade coll. (BCPM 978-180, several specimens).

DESCRIPTION: All animals are broken; the largest and thickest specimen, with 20 abdominal segments, is almost 2 cm long. Three specimens each possess 12 and 13 thoracic setigers, starting from segment 3 (determined from location of nephridial papillae on setigers 4–6 in one animal). The tentacular membrane is medium-sized, three-lobed, and bears two kinds of tentacles but no eyes. The thoracic and abdominal segments are biannulate. The dorsally elevated thoracic epidermis is further divided by transverse rings and longitudinal lines into small rectangles of varying size. Ventrally (Fig. 8E), segment 1 (and 2?) forms the anterior central pad; laterally, another glandular area is distinct anterior to the pads of segment 2. The paired glandular pads are large and cover the entire ventral surface through setiger 6; smaller pad-like areas are developed on the following two or three setigers.

The notopodia (Fig. 8F) are conspicuous and often have slightly thickened lips above the dorsalmost setae, distinct in undissected material. The setae are narrowly limbate and bear hairs near the tips which are visible only under an oil immersion lens (Fig. 8G). Neuropodial lobes are externally visible only two to three segments past the last one with notosetae and carry long rows of uncini; animals were not dissected, however, to check for withdrawn, rudimentary neuropodia anteriorly. The uncini are characterized by numerous small teeth above and to the side of the secondary tooth (Fig. 8H, I).

Dissection revealed three anterior, large nephridia and three posterior small ones.

Scionides Chamberlin

Scionides Chamberlin, 1919a:421 — Hartman 1959: 521 — Fauchald 177:132 [all in part].

TYPE SPECIES: *Terebella reticulata* Ehlers.

REMARKS: On the basis of observations by Hartman (1938) on the type species, and additional ones reported below, the generic diagnosis must include "Notosetae serrated" instead of "Notosetae smooth" as stated by Chamberlin (1919a) and Fauchald (1977).

The genus is included among the Amphitritinae without lateral lobes that have three pairs of gills and considerably more than 17 thoracic setigers. Hessle (1917) and Hartman (1938) surmised that the type species of *Scionides* might belong to *Neoamphitrite* where the numbers of thoracic setigers may vary (cf. *N. groenlandica* [Malmgren]). The form of the uncini described herein for the type species, however, is different from that found in members of *Neoamphitrite*. *Scionides* may thus be retained, primarily on the strength of the diagnostic characters stressed by Ehlers (1887:248) for separating his *Terebella reticulata* from the other species of *Terebella*; those generic characters used by Chamberlin (1919a) that are still valid are less pertinent.

The only other species assigned to *Scionides*, *S. dux* Chamberlin, has been placed in synonymy with *Neoamphitrite robusta* (see above).

Scionides reticulata (Ehlers)

Fig. 8J, K

Terebella reticulata Ehlers, 1887:245 — Hessle 1917:184 — Chamberlin 1919a:421; 1919b:266 — Hartman 1938:18.

Scionides reticulata — Hartman 1959:521; 1969:637 [under *Scionides dux*].

MATERIAL: Florida (MCZ 840; holotype).

ADDITIONS TO THE DESCRIPTION: Ehlers (1887) was uncertain about the form of the notosetae. Hartman (1938), however, observed in the type that they are distally denticulate. After having found only one seta remaining, I confirm that the notosetae are serrated and add that they are twisted at the tips (Fig. 8J); the serration continues on the twisted section. Further, the uncini differ from Ehlers' (1887) description: Thoracic and abdominal uncini have a rounded base (Fig. 8K).

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Production of Nonviable Oocytes by Pacific Hake (*Merluccius productus*)

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FOUCHER, R. P., AND R. J. BEAMISH. 1980. Production of nonviable oocytes by Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 37: 41–48.

Ripening ovaries of Pacific hake from the Strait of Georgia contained several size-classes of oocytes. Only those from the group of the largest yolked oocytes became hydrated and were eventually released to be fertilized. Examination of ovaries from recently spawned fish showed that smaller, residual yolked oocytes were being resorbed. Yolked oocytes not released at spawning may represent a potential for an increase in fecundity of Pacific hake in the Strait of Georgia. The failure of some developing oocytes to be released suggests that traditional methods of estimating fecundity will not accurately estimate the number of gametes produced by each female. Cytological observations suggested that the number of potential oocytes is not fixed at first maturity.

Key words: Pacific hake, fecundity, oocytes, spawning, Strait of Georgia

FOUCHER, R. P., AND R. J. BEAMISH. 1980. Production of nonviable oocytes by Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 37: 41–48.

Les ovaires en voie de maturation de merlus du Pacifique capturés dans le détroit de Géorgie contenaient plusieurs classes de taille d'ovocytes. Seuls ceux provenant du groupe qui contenait le plus de vitellus s'hydratèrent et furent ensuite libérés pour être fécondés. Un examen des ovaires de poissons ayant frayé récemment indique que les petits ovocytes avec vitellus résiduaire sont résorbés. Les ovocytes contenant du vitellus qui ne sont pas libérés au moment de la fraie sont une source possible d'augmentation de fécondité du merlu du Pacifique dans le détroit de Géorgie. Le fait que quelques ovocytes en voie de développement ne sont pas libérés donne à penser que les méthodes traditionnelles d'estimation de la fécondité ne donnent pas de résultats précis quant au nombre de gamètes produites par une femelle. Des observations cytologiques suggèrent que le nombre d'ovocytes potentiel n'est pas fixé lors de la première maturité.

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STATE of maturity observations of Pacific hake in the Strait of Georgia during the spawning period revealed that oocytes did not exhibit synchronous development, suggesting that not all oocytes would be released as viable gametes at the same time. This study was undertaken to demonstrate whether the unspawned oocytes were resorbed or continued to develop and become viable in some subsequent spawning period. The term viable is used to identify developing oocytes which are spawned.

Materials and Methods

Pacific hake were collected in the Strait of Georgia (49°N; 123°W) throughout all seasons during 1974–78, by midwater and bottom trawls. Results of cruises and methods of collecting have been described in a series of data records published by the Fisheries and Marine Service (Beamish et al. 1978a; Weir et al. 1978; and others). Ovaries were selected to represent all the maturity states of hake described by Foucher and Beamish (1977). Samples were preserved in Bouin's fixative (1 part glacial acetic acid, 5 parts formalin, 15 parts 1.2% saturated aqueous solution of picric acid) and stored in 95% ethanol. Cross sections, 6 μm in thickness, were cut from the middle portion of the ovary mounted in 61°C paraffin. Sections were stained for 4 min in Harris' haemotoxylin followed by a 30-s counterstain in 0.5% eosin in 95% ethanol.

Oocyte diameters were calculated as the mean of the minimum and maximum diameters. These were measured either from a television screen connected to a closed-circuit, television-microscope system or from photographic enlargements. Cell measurements made using these two methods were compared by measuring the same sample of cells using each technique. The precision of the diameter measurements was checked by having each of two technicians measure cells from one slide. The Kolmogorov-Smirnov two-sample test (Fisz 1963) was used to determine if significant differences existed between the two measurements.

To ensure that measured oocyte diameters would be relatively close to the true oocyte diameters, we measured only oocytes whose nuclei were included in a section (except for resorbing and translucent oocytes whose nuclei were broken down). An empirical test of the error involved in using the diameter of a cell measured from a section as a measure of its true diameter was made by examining serial sections from the same ovary. Cells that had been

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sectioned through the nucleus were measured from one section and their true diameters were determined from adjacent serial sections.

Because the nucleus of resorbing oocytes and the nuclear membrane of hydrated oocytes deteriorated quickly, all resorbing and hydrated (translucent) oocytes were measured with the knowledge that measurement error (underestimation of actual diameter) was increased.

The probability of an oocyte being in a section and it being included in the results (nucleus also in section) is proportional to the diameter of its nucleus which increases much less than the cell's diameter. If cells not sectioned through the nucleus had been included, the probability of a cell being measured would be proportional to its diameter and the larger cells would have been favored. By including only cells showing a nucleus, bias towards larger cells was minimized as the increase in diameter of the nucleus was relatively small.

Results

The accuracy of the diameter measurement was tested by determining the true diameter from serial sections of 41 oocytes. The average underestimate of the true diameter by measuring any cell that contained a nucleus was found to be 5.4%. Thus the procedure of using measurements of only those cells having nuclei to approximate oocyte diameters was considered representative of the true diameter of the oocyte. Because the difference in diameter of cells in distinct modes is commonly 100–200 μm or more this error does not appreciably affect the relative position of the modes. The very small error associated with these measurements also indicates that the nucleus in the fixed cell tends to be at the center of the cell.

A comparison of diameter measurements from photographs and the closed-circuit television (Fig. 1A) indicated there was no significant difference between the two methods, $0.75 < P < 0.90$ (Kolmogorov-Smirnov test). There also was no significant difference in measurements made by two technicians (Fig. 1B) from the same slide, $0.50 < P < 0.75$ (Kolmogorov-Smirnov test).

Approximately 4000 mature female hake were checked for maturity from 1974 to 1978 and ovaries from 313 of these specimens were examined histologically. Oocyte diameters measured from a number of these show several modes (Fig. 2). The smallest mode consists of a large number of oocytes 50–150 μm in diameter and containing no yolk. These cells represent the reserve stock of young oocytes from which, each year, a proportion proceed with further growth and maturation. Expansion of the ovary due to an increase in diameter of the growing oocytes results in the small, nondeveloping oocytes being distributed through a considerably greater volume so that fewer of them occur in a section as the ovary matures. Because of the time required to measure the diameter of the large number of reserve oocytes they were included in only one figure (Fig. 2C). Oocyte measurements from each ovary were arranged according to advancing maturity rather than by time of sampling and were expressed as percent. A considerable range in maturity states, assigned macroscopically, was evident in individual samples (Fig. 3) and in some fish development was 2–3 mo later than most of the population (Fig. 2D, H, I).

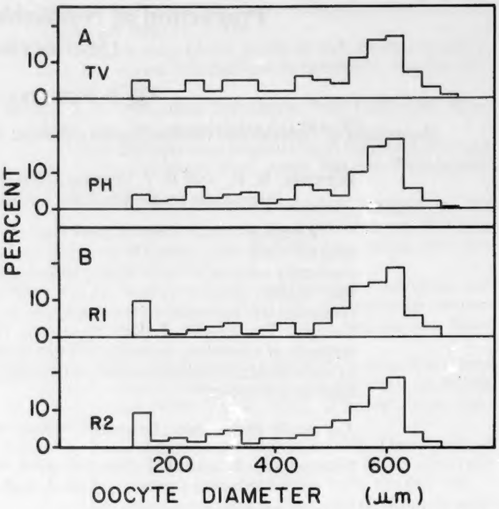

FIG. 1. A, Comparison of frequency (%) of Pacific hake oocytes measured from photographs (PH) and from closed-circuit television (TV). B, Comparison of frequency (%) of Pacific hake oocytes measured by two readers (R1 and R2).

Ovaries in early stages of development have a mode (150–300 μm) of small oocytes (Fig. 2A to D) which have begun to accumulate yolk. These are cells which have recently grown from the stock of reserve oocytes in preparation for spawning. They continue to increase in size (Fig. 2E to I) until the ripe stage at which there is a distinct mode of cells around 600 μm in diameter (Fig. 2J to Q). Prior to the ripe stage, it appears that asynchronous growth results in the appearance of modes of smaller yolked oocytes (300–450 μm).

Following the ripe stages, the more advanced oocytes hydrate and undergo a great increase in volume and diameter (Fig. 2S). This dilutes their contents causing them to become translucent in appearance. Pacific hake oocytes ready for release average slightly more than 1 mm in diameter and contain an oil globule about one third of a millimetre in diameter. The translucent oocytes, having undergone ovulation in preparation for spawning form a loose mass in the ovary. Gonad maturity data from an extensive collection in the Strait of Georgia during 1974–78 show a change from predominately ripe in late March to spent and recovering in late May (Fig. 3). Spawning begins in March and

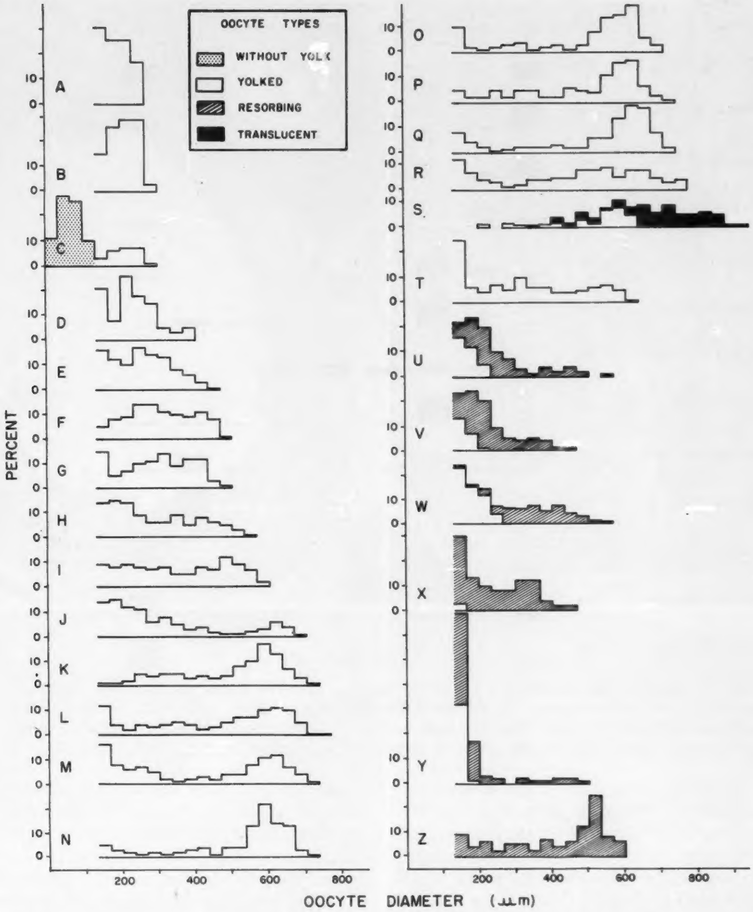

FIG. 2. Frequency (%) of Pacific hake oocytes diameters arranged in approximate order of increasing ripeness. Cells less than 140 μm not included except in C which shows relation of developing oocytes to reserve oocytes in early development. Sample sizes and dates indicated. A, Jan. 16, 1976, $n = 213$; B, Dec. 9, 1975, $n = 90$; C, Same section as B but with reserve oocytes included, $n = 359$; D, Apr. 2, 1976, $n = 39$; E, Jan. 13, 1976, $n = 482$; F, Jan. 16, 1976, $n = 275$; G, Jan. 16, 1976, $n = 99$; H, Apr. 2, 1976, $n = 591$; I, Apr. 2, 1976, $n = 791$; J, Mar. 25, 1976, $n = 563$; K, Mar. 25, 1976, $n = 482$; L, Mar. 30, 1976, $n = 417$; M, Mar. 25, 1976, $n = 542$; N, Mar. 30, 1978, $n = 358$; O, Mar. 31, 1978, $n = 272$; P, Mar. 30, 1978, $n = 368$; Q, Mar. 30, 1978, $n = 333$; R, Mar. 25, 1976, $n = 199$; S, Mar. 25, 1976, $n = 150$; T, Mar. 31, 1978, $n = 260$; U, May 30, 1977, $n = 255$; V, May 30, 1977, $n = 938$; W, May 30, 1977, $n = 328$; X, May 30, 1977, $n = 364$; Y, May 30, 1977, $n = 180$; Z, June 10, 1976, $n = 85$.

peak spawning occurs in April or May. Ichthyoplankton studies indicate that a peak concentration of hake eggs in 1979 occurred in the first week of April (J. C. Mason, personal communication, Pacific Biological Station, Nananimo, B.C.), supporting the spawning period suggested by macroscopic observations of ovaries.

Observations of recently spawned ovaries indicated that a large volume of macroscopically visible, non-hydrated oocytes (400–600 μm in diameter) frequently

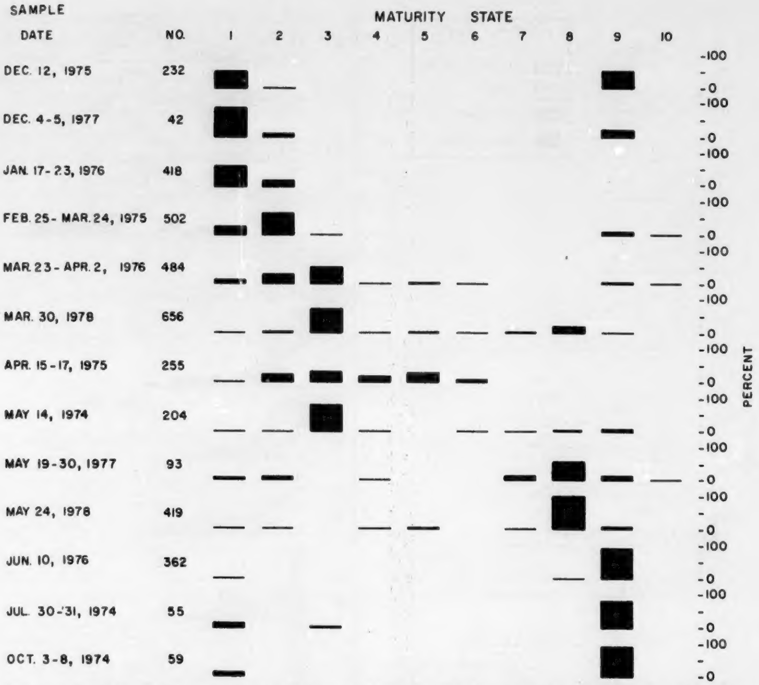

FIG. 3. Pacific hake maturities (%) by sample, 1974–78 Strait of Georgia. Maturity states: 1, early development; 2, advanced development; 3, Ripe; 4, less than one half the oocytes hydrated; 5, more than one half hydrated; 6, sex products flow freely from vent; 7, Spent; 8, Recovering; 9, Resting; 10, Resorbing (resorption without spawning).

remained after spawning (Fig. 2T). These ovaries are similar in appearance to those in early stages of development but may be distinguished microscopically by the few remaining translucent oocytes and numerous empty follicles. Soon after spawning resorption of all remaining yolked oocytes begins. Recovering ovaries examined from fish sampled in May contained many resorbing oocytes of various sizes (Fig. 2U to Y). Resorption of most yolked oocytes and empty follicles is fairly rapid but a few form temporary structures thought to have possible endocrine functions and a role in preventing development for a second spawning (Christiansen 1971).

Occasionally ripe ovaries from fish that had not spawned were collected soon after most of the stock had spawned; these were completely resorbing their ripe ovaries (Fig. 2Z).

Once resorption is complete all that remains is the smallest oocytes, making up the reserve stock for future spawnings. At this point the ovary enters a resting state, common from June to October (Fig. 3). Of 42 ovaries examined that were resting or just beginning development (collected from May to early December), none was found to contain oocytes greater than 225 μm in diameter.

After each follicle bursts at ovulation to release its enclosed oocyte it collapses into an irregular mass and is usually quickly resorbed. In some spent ovaries, however, empty follicles were seen which had shrunk to a smaller size while retaining their spherical shape (Fig. 4A). An apparent increase in the number of cells in the follicle results in a much thickened follicular layer and the formation of large masses of cells, each cell being 4–8 μm in diameter with no cytoplasm, but visible chromatin (Fig. 4B). The obvious concentration of chromosomes in many of these cells suggests that they are in the synaptic stage of early meiosis (Fig. 4C). In some recovering ovaries these 4–8 μm diameter cells, which might be termed follicular oocytes, occupied the greater part of the volume of the ovary (Fig. 4D). Follicular oocytes were seen in spent, recovering, and resting ovaries sampled from March to June and were often associated with the occurrence of empty follicles, the remains of unspawned translucent oocytes, and resorbing, yolked oocytes. A few ovaries sampled in December contained these cells, perhaps due to mixing of stocks or anomalous development of individual fish.

Diameter-frequencies of two resting ovaries sampled in June (Fig. 5A, B) contain two modes. The smaller mode (10–20 μm) appears to be made up of follicular

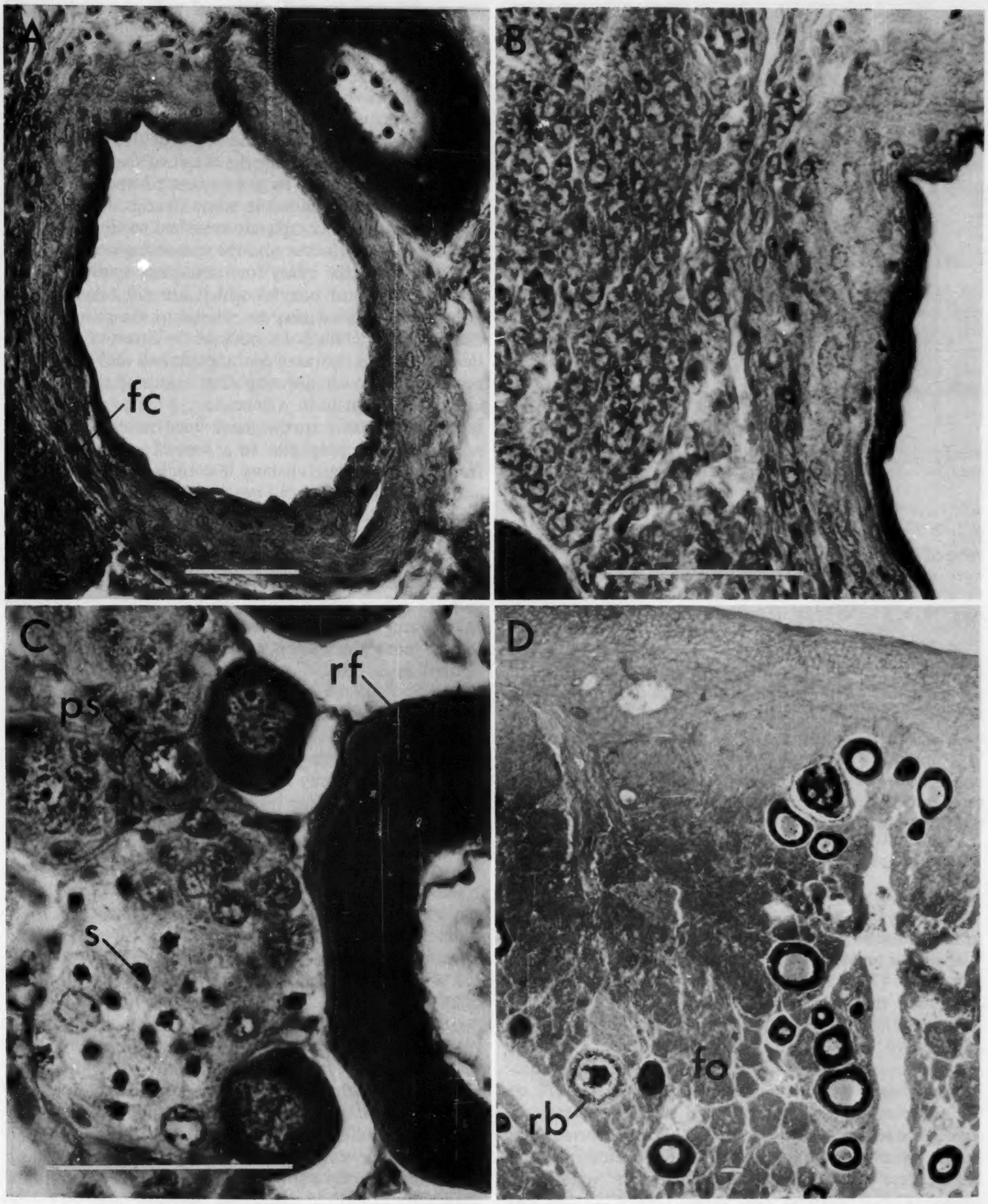

FIG. 4. A, Thickened layer of follicle cells (fc) from empty follicle not undergoing usual collapse and resorption. B, Mass of cells appearing to be derived from cells of empty follicles. C, Oocytes of follicular origin in synaptic stage (s) and post-synaptic oocytes (ps) growing to join reserve cells (rf). D, Groups of follicular oocytes (fo) filling most of ovary which also contains reserve oocytes and a few resorbing structures (rb). Bar = 50 μm.

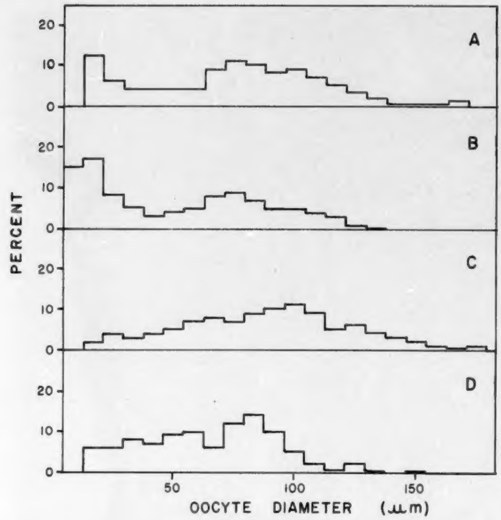

FIG. 5. Frequency (%) of oocyte diameters in undeveloped ovaries. Smallest cells (not included in Fig. 2) were measured at higher magnification. A, resting, June 1976, $n = 279$; B, resting, June 1976, $n = 459$; C, resting, Aug. 1977, $n = 491$; D, immature, Dec. 1975, $n = 507$.

oocytes which are passing, or have passed, through synapsis, one of the early stages of the meiotic process, and are increasing in size to join the stock of reserve oocytes. In a resting ovary sampled in August (Fig. 5C) the smaller cells of the first mode are missing, and presumably have grown to join the mode of larger reserve oocytes from which the next year's crop will later develop.

Discussion

Multiple size modes of oocytes have been interpreted in some studies as indicating multiple spawnings in one year or the presence of "year-classes" of oocytes within the ovary (Nikolskii 1969). Ermakov et al. (1974) concluded that Pacific hake found off the west coast of the northern United States spawn in stages with two clutches of eggs relased each year. They measured oocyte diameters from 45 ovaries collected in November and found that a single mode occurred in 22% of the samples, 65% were bimodal and 6% were trimodal. MacGregor (1966; 1971) also reported that oocyte diameters from Pacific hake collected off California were multimodal. Fish sampled in April, after spawning, had retained their small, yolked oocytes and it was stated that these must be resorbed although no histological evidence was presented. MacGregor concluded that the apparently poor condition of the fish after spawning would make it improbable that these fish could produce the volume of yolk material necessary for the development of the smaller oocytes for a second spawning. Although data on condition were not reported, the apparent condition and lack of any evidence of a second spawning in the plankton resulted in the conclusion that Pacific hake in these regions spawn only once a year. The study of oocyte development of Pacific hake from the Strait of Georgia clearly showed that relatively large numbers of small and large yolked oocytes remained in some ovaries after spawning but they were completely resorbed so that a second spawning did not occur and the remaining oocytes were not "stored" in the ovary for subsequent spawning.

The number of oocytes which are not released and are finally resorbed may be related to the general condition of the Pacific hake stock in the Strait of Georgia. Pacific hake in this area are unexploited and have been noted to be slower growing after maturity than Pacific hake found offshore (Beamish 1979). Increases in fecundity in other species have been related to an improved food supply due to a reduction in stock size from a commercial fishery (Woodhead 1960; Tyler and Dunn 1976). It is possible, then, that a future fishery for Pacific hake in the Strait of Georgia will reduce the stock size, resulting in an increase in the individual production of viable oocytes and a simultaneous decrease in production of nonviable oocytes.

Although it seems probable that individual Pacific hake found off the west coast of North America do not spawn more than once a year, it has been reported (Christiansen and Cousseau 1971) that *Merluccius merluccius hubbsi* in the Argentine Sea spawn more than once a year. While Christiansen and Cousseau (1971) believed that a portion of the summer (October–March) spawning stock spawned again in the winter (June–July), they acknowledged the possibility that they might be studying more than one stock. It was not actually demonstrated that individual hake spawned more than once a year and there is the possibility that more than one stock is involved.

Stocks of Pacific hake in the Strait of Georgia do exhibit variation in spawning times. Some fish from what appears to be a small stock of much larger Pacific hake in the Gulf Islands near Yellow Point (49°03′N, 123°45′W) have been observed to spawn 5–6 mo prior to the main stock (Beamish et al. 1978b) indicating there can be extreme variability of spawning times within a small area. Thus, although there was no evidence in the present study that any individual fish spawned more than once in one year, it is possible that multiple spawnings within the same area occur in one year. Our results show that it is necessary to examine the oocyte development of individuals from the same stock throughout the year before cases of multiple spawnings of individual fish can be confirmed.

The occurrence of large, yolked oocytes remaining in the ovaries of Pacific hake from the Strait of Georgia after spawning may introduce an error (overestimate) in estimates of oocyte production by conventional techniques of evaluating fecundity. Fecundity has been defined as "the number of eggs (oocytes) for the generation of that year present in the ovaries, i.e. the number that should be laid in that year" (Nikolskii 1965). The difficulty with this and similar definitions is that it may not be possible to differentiate the oocytes that are "for the generation of that year" since many may be retained in the ovary after spawning. Absence of an obvious relation between the number of oocytes counted and the number of viable oocytes that are ultimately released indicates that the assumptions used when making fecundity measurements must be clearly identified when applying these measures to Pacific hake and perhaps other species. Fecundity should be defined as the number of oocytes that are actually released to be fertilized, i.e. the number of viable oocytes. Because it is difficult to differentiate and count viable oocytes prior to spawning, studies of fecundity should include, along with the traditional counting methods, a histological examination of spent and recovering ovaries from fish of the same stock to determine the relationship between the proportions of viable and non-viable oocytes. An increase in fecundity might be brought about by an increase in the proportion of developed oocytes that become viable and are released rather than by an increase in the number of oocytes which began developing that season. Since the fecundity methods now in use cannot distinguish viable from non-viable oocytes they might not detect such an increase.

It is not known how the total fecundity over the reproductive lifespan of a fish is controlled. Although various theories exist (Foucher and Beamish 1978), it is not certain whether new gametes are produced to supplement the stock of reserve oocytes after first maturity or if the total number of germ-cells are present at first maturity.

In hake, oogonial divisions are completed before first maturity and the newly mature ovary is full of the resulting resting oocytes (Hickling 1930). Many of these young oocytes grow to form a reserve from which a portion develop for spawning in each year after maturity. Results of this study indicate a growth of young oocytes to join the reserve stock in the mature resting ovary. The question, often raised, is whether the number of resting oocytes present is sufficient for the replacement of oocytes removed annually from the reserve stock for reproduction. Hickling (1930) theorized that there exists a vast number of resting oocytes within the ovigerous lamellae of the newly mature ovary of *M. merluccius* sufficient in number to maintain the reserve stock throughout the fish's reproductive lifespan so that a further production of oocytes is unnecessary. Wheeler (1924) suggested that the reserve stock of oocytes are added to by growth of certain of the follicle cells, known to be sister-cells of the oocytes. Cytological evidence presented in the current study indicates the possibility that, in Pacific hake, the reserve stock is supplemented by cells that are produced from the remains of empty follicles. Observations on time of occurrence of this production of follicular oocytes suggest an annual process. Because it is not always seen in recovering ovaries, it is either a short-term event or it may not occur in all fish each year. Although little is known of the conditions for, or frequency of, occurrence of this process, it is a possible mechanism for a complete restocking of the reserve stock of oocytes. That is, the number of gametes is not fixed at the time of first maturity, but is restocked, perhaps on an annual basis.

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New and Rare Records of Canadian Fishes and the Influence of Hydrography on Resident and Nonresident Scotian Shelf Ichthyofauna

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A recently initiated ichthyoplankton survey of the Scotian Shelf has discovered large numbers of subtropical/tropical expatriated fishes, mostly larvae, and at least two previously unrecognized populations. Thirty-three species in 25 primarily subtropical families (Carcharhinidae, Engraulidae, Synodontidae, Chlorophthalmidae, Ogcocephalidae, Antennariidae, Carapidae, Ophidiidae, Exocoetidae, Syngnathidae, Scorpaenidae, Triglidae, Dactylopteridae, Serranidae, Apogonidae, Branchiostegidae, Rachycentridae, Sciaenidae, Labridae, Scaridae, Callionymidae, Gobiidae, Bothidae, Cynoglossidae, and Ostraciontidae), seven species in four deepwater families (Gonostomatidae, Sternoptychidae, Myctophidae, and Moridae) and two gadoids are reported as new or rare records from the Canadian Atlantic. The frequency and quantity of subtropical expatriates raise the question of their ultimate fate. The existence of eastern Atlantic populations of some of these raises the possibility of transatlantic dispersal. Juvenile or adult specimens of most of the expatriated forms have not been found on the Scotian Shelf but the complex hydrography on the shelf may allow temporary habitation especially in summer. Two species, red hake and Gulf Stream flounder, appear to have discrete, self-sustaining populations on the Scotian Shelf. Both species appear to represent northernmost populations which may be living near their lower thermal limit. Discrepancies between the literature on red hake and data reported herein are unresolved and require long-term observations.

Key words: Scotian Shelf, ichthyoplankton, hydrography, zoogeography, western North Atlantic

MARKLE, D. F., W. B. SCOTT, AND A. C. KOHLER. 1980. New and rare records of Canadian fishes and the influence of hydrography on resident and nonresident Scotian Shelf ichthyofauna. Can. J. Fish. Aquat. Sci. 37: 49–65.

Au cours d'un relevé ichtyoplanctonique récemment entrepris sur le plateau continental Scotian on a découvert un grand nombre de poissons subtropicaux/tropicaux expatriés, larves pour la plupart, et au moins deux populations ignorées jusqu'à maintenent. Nous signalons comme mentions nouvelles ou rares en Atlantique canadien 33 espèces appartenant à 25 familles principalement subtropicales (Carcharhinidae, Engraulidae, Synodontidae, Chlorophthalmidae, Ogcocephalidae, Carapidae, Ophidiidae, Exocoetidae, Syngnathidae, Scorpaenidae, Triglidae, Dactylopteridae, Serranidae, Apogonidae, Branchiostegidae, Rachycentridae, Sciaenidae, Labridae, Scaridae, Callionymidae, Gobiidae, Bothidae, Cynoglossidae et Ostraciontidae), sept espèces appartenant à quatre familles de profondeur (Gonostomatidae, Sternoptychidae, Myctophidae et Moridae) et deux gadoïdes. La fréquence et la quantité d'expatriés subtropicaux soulève la question de leur sort ultime. Comme il existe des populations de quelques-unes de ces espèces en Atlantique oriental, il est possible qu'il y ait dispersion transatlantique. On n'a pas trouvé de jeunes ou d'adultes de la plupart des formes expatriées sur le plateau Scotian, mais il se peut que les conditions hydrographiques complexes du plateau continental offre un habitat temporaire surtout en été. Deux espèces, la merluche rouge et la plie du Gulf Stream, semblent avoir sur le plateau Scotian des populations distinctes et autonomes. Les deux espèces semblent représenter les populations les plus septentrionales qui vivent peut-être près de leur limite thermale inférieure. Nous ne pouvons concilier le désaccord entre ce qui a été déjà publié sur la merluche rouge et les données contenues dans le présent article; il faudra pour cela des observations à long terme.

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ONE of the commonly stated goals of larval fish surveys is to detect the presence of members of the ichthyofauna that might otherwise go unnoticed (Ahlstrom and Moser 1976). In many cases pelagic larvae are more vulnerable to plankton nets than the adults are to other fishing gears. In addition, the planktonic larvae, as the dispersal phase in many life histories, can be the only life history stage found in an area that is otherwise unsuitable for juveniles or adults.

Largely as a result of extended fisheries jurisdiction, the Marine Fish Division of the Canadian Department of Fisheries and Oceans (MFD–DFO) has set up an extensive ichthyoplankton survey of the Scotian Shelf. Most of the present report is based on the initial "shake-down" cruises of the Scotian Shelf Ichthyoplankton Program (SSIP). In addition, one of us (W. B. Scott) has been collecting distributional information on Canadian Atlantic fishes in preparation for his revision of *Fishes of the Atlantic Coast of Canada* (Leim and Scott 1966) and some of these records are included herein.

Materials and Methods

The SSIP samples of primary concern are those from *E. E. Prince* cruises P170 (August 12–24, 1976) and P182 (April 30–May 19, 1977), *Canso Condor* cruise CC01 (February 15–March 26, 1977) and *Canso Light* cruise CL01 (August 8–September 2, 1977). These cruises normally followed a 159-station stratified random sampling program over the Scotian Shelf (Fig. 1).

During these cruises up to five different plankton nets were used with mesh sizes as follows: bridled ring meter net with 0.471 mm Nitex; 61 cm bongo nets each with 0.471 mm Nitex; 1 m wide neuston net with 1.179 mm Nitex main body and 91 cm tail section of pattern 1400 white knotless nylon; 1.83 m modified Isaacs-Kidd midwater trawl (IKMT), first section of bag interliner of 13 mm stretched mesh knotless nylon, aft tube of 10 mm stretched mesh knotless nylon, 0.5 m codend of 0.471 mm Nitex; and high speed Miller samplers constructed from 66 cm long fiberglass tubes with 10.2 cm internal diameter mouth opening increasing to 14.0 cm aft with a codend of 0.471 mm Nitex.

Meter nets were towed at the surface for 30 min at 2.5 knots (kn) (range 1.5–5.5 kn). Neuston nets were towed at the surface for 30 min at 5.0 kn (2.5–6.0 kn). Miller samplers were towed in series at depths of about 0, 9, 18, 27, 36, 46, and 55 m for 30 min at 2.5 kn only on cruise P182. Bongo nets were towed for 30 min obliquely in steps from near the bottom to the surface at 2.5 kn (1.5–5.5 kn). IKMT was towed for 30 min obliquely in steps from near the bottom to the surface at 5.0 kn (2.5–6.0 kn).

Data are also reported herein from groundfish cruises on the Scotian Shelf made aboard the vessels *A. T. Cameron*, *P. J. Lawrence*, and *Lady Hammond*.

Results

The following list of species is arranged following the classification of Greenwood et al. (1966) as subsequently modified by Rosen (1973) and Nelson (1976). Following each species we record, where available, the museum number or HML sample catalog number, number of specimens, standard length (SL) or range of SL, vessel and/or cruise number, station and/or set number, coordinates, date, time, gear, and gear depth.

Institutional abbreviations used are: HML — Huntsman Marine Laboratory, St. Andrews, New Brunswick; NMC — National Museum of Natural Sciences, National Museums of Canada, Ottawa, Ontario; and ROM — Royal Ontario Museum, Toronto, Ontario. Abbreviations used for taxonomic characters are: TL — total length, SL — standard length, HL — head length, D — number of dorsal fin rays, A — number of anal fin rays, P_1 — number of pectoral fin rays, P_2 — number of pelvic fin rays. Photophore abbreviations are: IC — number in ventral series, IV — prepelvic number in ventral series, OA — number in lateral

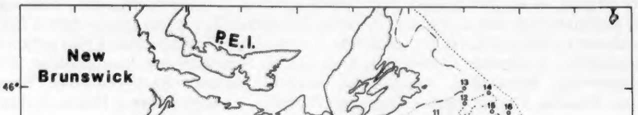

FIG. 1. Scotian Shelf showing location and station numbers during cruise CL01.

series, AC — postanal number in ventral series, and BR — number on branchiostegal membranes.

ORDER SQUALIFORMES

Family CARCHARHINIDAE

Mustelus canis (Mitchill) (smooth dogfish) — ROM 35140, 1 specimen 1065 mm, female, Bay of Fundy off Chance Harbour, New Brunswick 45°07′N 66°14.5′W, July 8, 1977, caught by hook and line. The specimen was transported alive from Chance Harbour to St. Andrews and gave birth to three young en route, TL 328, 330, 335. All four specimens were retained alive for a short time in the HML aquarium, the adult for 9 d. All specimens were preserved.

Mustelus canis occurs regularly south and west of Cape Cod but rarely north of the Cape and only once before in Canadian waters. Huntsman (1922) recorded a specimen caught in July 1913 in the estuary of the St. Croix River, Passamaquoddy Bay, only about 35 mi east of the present record.

Mustelus canis is undoubtedly rare in the area but it may occur more often than present records would indicate. It is probable that the casual observer would mistake *M. canis* for the ubiquitous spiny dogfish, *Squalus acanthias.*

ORDER CLUPEIFORMES

Family ENGRAULIDAE

Eugraulis eurystole (Swain and Meek) (silver anchovy) — HML — H2619, 3 specimens 18.0–18.3 mm, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, 0225 h, IKMT, 144 m. HML — H2643, 1 specimen 25.3 mm, CL01, st 106, set 62, 42°48′N 63°28′W, August 16, 1977, 1650 h, IKMT, 282 m. HML — H2647, 1 specimen 26.7 mm, CL01, st 88, set 66, 43°02′N 62°02′W, August 17, 1977, 0235 h, IKMT, 124 m. HML — H2649, 1 specimen 28.3 mm, CL01, st 73, set 68, 43°06′N 61°30′W, August 17, 1977, 0645 h, IKMT, 282 m. HML — H2722, 1 specimen 28.0 mm, CL01, st 50, set 142, 43°35′N 59°28′W, August 31, 1977, 0650 h, IKMT, 188 m. HML — H2773, 1 specimen ca. 24.0 mm, CL01, st 135, set 35, 42°35′N 65°00′W, August 14, 1977, 0015 h, neuston, surface. HML — H2774, 1 specimen mutilated, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, 0225 h, neuston, surface. NMC 78-284, 3 specimens 24.0–29.0 mm, CL01, st 90, set 64, 42°47′N 62°38′W, August 16, 1977, 2145 h, neuston, surface. HML — H2803, 2 specimens ca. 25 and 29.3 mm, CL01, st 91, set 65, 42°58′N 62°28′W, August 16, 1977, 0015 h, neuston, surface. HML — H2804, 3 specimens 25.9–30.7 mm, CL01, st 88, set 66, 43°02′N 62°02′W, August 17, 1977, 0235 h, neuston, surface. HML — H2930, 2 specimens 16.4–18.0 mm, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, 0225 h, bongo, 119 m. HML — H3087, 1 specimen, 20 mm, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, 0225 h, meter net, surface. HML — H3118, 1 specimen, 29.0 mm, CL01, st 89, set 67, 42°57′N 61°44′W, August 17, 1977, 0405 h, meter net, surface. HML — H3116, 2 specimens, CL01, st 91, set 65, 42°58′N 62°29′W, August 16, 1977, 2345 h, meter net, surface. HML — H3127, 2 specimens CL01, st 100, set 76, 43°51′N 63°00′W, August 16, 1977, 0020 h, meter net, surface.

The eggs and larvae up to 5.2 mm TL were described by Kuntz and Radcliffe (1917) and adults 55–130 mm SL by Hildebrand (1963) and others. A 22.8 mm TL specimen was illustrated by Lippson and Moran (1974). Our material includes part of the size range, 16.4–30.7 mm SL, which has not been described. Meristics of two cleared and stained specimens agreed with Hildebrand's description. Counts from H2722 and H2773 were: D 15, A 15–18, preural vertebrae 25–26 + 18 = 43–44, branchiostegal rays 11, gill rakers on upper and lower limbs of first arch 7 + 16-development incomplete (H2773) and 10 + 17 (H2722). The largest specimens (>24 mm) have an overhung snout and lack an adipose fin as is typical of engraulids.

In our smallest specimens, 16.4–18.4 mm SL (Fig. 2A), the vertical fins are completely formed with the adult complement of fin rays and the paired fins are formed but undeveloped. The gas bladder is prominent in all specimens less than 29 mm SL. Smaller specimens have a prominent midventral row of melanophores on the isthmus, a few cheek melanophores, and rows dorsolateral to the intestine, above the anal fin and ventrally on the caudal peduncle (Fig. 2A). Pigmentation becomes denser in larger specimens with melanophores forming on the head, along the midlateral line, on the caudal fin rays and internally, along the neural arches and dorsal peritoneum (Fig. 2B). These larger specimens bear a superficial resemblance to Atlantic menhaden (*Brevoortia tyrannus*) of similar size (Hildebrand 1963), but are easily distinguished by the longer upper jaw. According to Hildebrand's (1963) keys, these larger specimens agree with *Anchoviella eurystole.* Whitehead (1964) and Berry (1964) have subsequently referred *eurystole* to *Engraulis.*

Engraulis eurystole has been reported from Woods Hole, Massachusetts, to Beaufort, North Carolina (Hildebrand 1963). Daly (1970) tentatively identified a single specimen from Miami, Florida and Klima (1971) reported occasional specimens from bottom trawls and nightlight stations in the northern Gulf of Mexico. It is perhaps indicative of this species' ability to avoid nets that most of our specimens were also caught at night and in our larger nets (IKMT and neuston).

It has been repeatedly stated that *E. eurystole* inhabits the Gulf Stream, but its life history is unknown (Hildebrand 1963). All of our specimens were captured over the continental slope, in the Slope Water zone partly formed by the western edge of the Gulf Stream (see below). The absence of larger specimens from our collections may indicate that these specimens are expatriates or that the adults are better able to avoid

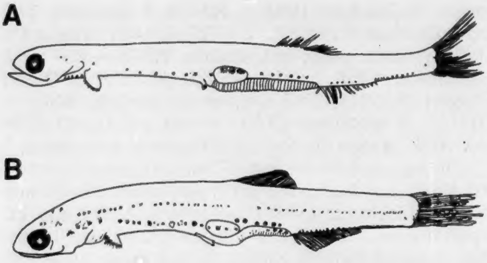

FIG. 2. A, *Engraulis eurystole*, HML-H2930, 18.0 mm SL, left lateral view; B, *Engraulis eurystole*, HML-H2802, 27.4 mm SL, left lateral view.

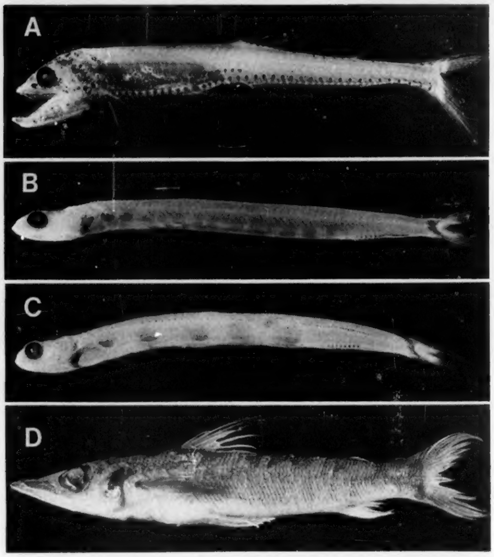

FIG. 3. A, *Pollichthys mauli*, NMC 78-280, 39.2 mm SL, left lateral view; B, *Synodus synodus*, NMC 78-282, 35.8 mm SL, left lateral view; C, *Trachinocephalus myops*, NMC 78-276, 39.5 mm SL, left lateral view; D, *Parasudis truculenta*, NMC 78-285, 186 mm SL, left lateral view.

the gear than other fishes of comparable size, such as sauries and myctophids, which are routinely captured. Alternatively, the adult habitat may be further south or further offshore than our sampling stations. These specimens represent a northern range record for the species and the first specimens from the Canadian Atlantic.

ORDER STOMIATIFORMES

Family GONOSTOMATIDAE

Pollichthys mauli (Poll) — NMC 78-280, 1 specimen 39.2 mm, CC01, st 137, set 168, 42°09′N 65°29′W, March 22, 1977, 1610 h, neuston, surface.

The identification is based on the keys and description in Grey (1964). Selected meristics: D 11, A 24, P_2 7; (photophores) — IC 49, IV 22, OA 20, AC 20, and BR 8 (Fig. 3A).

Pollichthys mauli is mesopelagic, commonly collected at 100–200 m at night and 200–500 m by day (Witzell 1973). Although unusual for being collected at the surface during daylight, our specimen is within the known geographic range near the northern range limit (Witzell 1973). However, it is apparently the first specimen from the Canadian Atlantic.

Cyclothone alba Brauer — HML — H1084, 1 specimen, CC01, st 35, set 45, 44°08′N 58°03′W, February 23, 1977, 0842 h, bongo, 527 m. HML — H1148, 1 specimen, CC01, st 126, set 111, 43°29′N 64°38′W, March 9, 1977, 1615 h, bongo, 59 m. NMC 78-278, 2 specimens, 20.8 and 24.1 mm, CC01, st 23, set 40, 44°14′N 57°35′W, February 20, 1977, 2050 h, bongo, 556 m. HML — H2645, 2 specimens ca. 14 mm, CL01, st 90, set 64, 42°47′N 62°38′W, August 16, 1977, 2145 h, IKMT, 282 m. HML — H3025, 1 specimen ca. 30 mm, CL01, st 158, set 132, 44°27′N 56°49′W, August 30, 1977, bongo, 412 m. HML — H3041, 1 specimen, ca. 13 mm, CL01, st 154, set 148, 43°48′N 58°42′W, September 1, 1977, bongo, 412 m.

The identifications are based on the descriptions of Bond and Tighe (1974) and Mukhacheva (1964).

Cyclothone alba is bathypelagic, commonly collected at 500–3000 m, and essentially cosmopolitan in tropical and subtropical latitudes (Witzell 1973; Badcock and Merrett 1977). These specimens apparently represent a northern range record for the species and the first specimens from the Canadian Atlantic.

Family STERNOPTYCHIDAE

Polyipnus asteroides Schultz — HML — H1294, 1 specimen 29.6 mm, CC01, st 90, set 88, 43°10′N 62°40′W, March 7, 1977, 0233 h, IKMT, 234 m.

The specimen agrees with the descriptions in Scott (1965) and Baird (1971).

Although only reported as far north as the Gulf of Maine by Baird (1971), this is the second capture of this subtropical hatchetfish on the Scotian Shelf (Scott 1965).

ORDER AULOPIFORMES

Family SYNODONTIDAE

Synodus synodus (Linnaeus) (red lizardfish) — NMC 78-282, 1 specimen 35.8 mm, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, 0225 h, IKMT, 144 m.

Gibbs' (1959) synopsis of synodontid postlarvae was the primary source for identifying synodontids. This specimen agrees exactly with *S. synodus*, having a single row of small palatine teeth, 9 anal fin rays, a pair of melanophores at the base of each of the last 6–7 anal fin rays, and 13 peritoneal spots (Fig. 3B).

Synodus synodus is primarily an inshore species found in the western Atlantic from the Gulf of Mexico, Bahamas, and Uruguay (Anderson et ai. 1966) and in the eastern Atlantic from Madeira and St. Helena (Nielsen 1973). According to Gibbs (1959) most synodontid postlarvae, with the exception of *Trachinocephalus myops*, are found over shallow water near land. However, Anderson et al. (1966) mention one 37.0 mm SL *S. synodus* from the 100 fm line off Cape Lookout, North Carolina. Our specimen from the continental slope off Nova Scotia and the Cape Lookout specimen suggest that some postlarvae of *S. synodus* are dispersed northward from the adult habitat by the Gulf Stream. Our specimen is a northern range record for the species and the first specimen from the Canadian Atlantic.

Trachinocephalus myops (Forster) (snakefish) — NMC 78-276, 1 specimen 40.8 mm, P170, st 19, set 19, 42°48′N 64°02′W, August 15, 1976, meter net, surface. HML — H2774, 1 specimen 38.4 mm, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, neuston, surface. HML — H2802, 1 specimen 42.0 mm, CL01, st 90, set 64, 42°47′N, 62°38′W, August 16, 1977, 2145 h, neuston, surface. HML — H3116, 1 specimen, CL01, st 91, set 65, 42°58′N 62°29′W, August 16, 1977, 2345 h, meter net, surface. HML — H3210, 1 specimen 38.9 mm, CL01, st 83, set 159, 44°06′N 62°00′W, September 2, 1977, meter net, surface.

The specimens agree with the description in Gibbs (1959). There are 14–15 anal fin rays, a pair of melanophores at the base of the last 5–8 anal fin rays, a row of discrete melanophores along the lateral line, pigment at the base of the adipose and the base of the caudal fin, five pairs of peritoneal spots and a pair of large branchial spots (Fig. 3C). Large postlarvae of *Argentina silus* are superficially similar to *T. myops* but can be distinguished by the position of the pelvics below the end of the dorsal fin and the absence of the adipose fin pigmentation.

Trachinocephalus myops is the most widespread synodontid, being almost circumtropical in distribution (Anderson et al. 1966). In the western North Atlantic, its most frequent adult habitat is the midcontinental shelf between North Carolina and Brazil, although it has been reported from Cape Cod (Anderson et al. 1966). In more recent cruises we have numerous multiple captures of snakefish. Our specimens represent a northern range record for the species and the first specimens from the Canadian Atlantic.

Synodus sp. — HML — H2619, 1 specimen 14.5 mm SL, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, 0225 h, IKMT, 144 m.

The pectoral and anal fin rays are not completely formed and so positive identification is not possible.

Family CHLOROPHTHALMIDAE

Parasudis truculenta (Goode and Bean) (longnose greeneye) — NMC 78-285, 1 specimen 186 mm, LH03, set 18, 42°46.8′N 63°58.1′W, July 15, 1978, 0210 h, 50 m Engels otter trawl, bottom, 249–273 m.

Identification of the specimen (Fig. 3D) is based on the key and description in Mead (1966).

Parasudis truculenta is known from Nantucket, Massachusetts, to the Gulf of Mexico and Caribbean Sea at depths of 183–480 m (Mead 1966). Our specimen is a northern range record and the first specimen from the Canadian Atlantic.

ORDER MYCTOPHIFORMES

Family MYCTOPHIDAE

All adult myctophids were identified using the keys and descriptions in Nafpaktitis et al. (1977).

Gonichthys coccoi (Cocco) — HML — H2867, 1 specimen 20.7 mm, CL01, st 156, set 130, 44°06′N 57°38′W, August 29, 1977, 2145 h, neuston, surface. HML — H2868, 1 specimen, CL01, st 157, set 131, 44°15′N 57°12′W, August 30, 1977, 0055 h, neuston, surface. HML — H2884, 17 specimens, CL01, st 153, set 147, 43°33′N 59°04′W, August 31, 1977, 2035 h, neuston, surface. HML — H2893, 1 specimen, CL01, st 173, set 156, 43°12′N 61°15′W, September 1, 1977, 2305 h, neuston, surface.

Gonichthys coccoi is a "tropical–subtropical," mesopelagic lanternfish most commonly collected in neuston samples at night (Krefft and Bekker 1973; Nafpaktitis et al. 1977). Our specimens are near the species' northwestern limit. It has previously been considered rare in the Canadian Atlantic (Leim and Scott 1966).

Hygophum benoiti (Cocco) — HML — H3040, 1 specimen, 26.5 mm, CL01, st 153, set 147, 43°32′N 59°06′W, August 31, 1977, 1952 h, bongo, 412 m.

Hygophum benoiti is a "temperate–semisubtropical" mesopelagic lanternfish (Krefft and Bekker 1973; Nafpaktitis et al. 1977). Our specimen is near the species' northwestern limit and is the second record from the Canadian Atlantic (Leim and Scott 1966).

Myctophum affine (Lütken) (metallic lanternfish) — HML — H2884, 2 specimens, 22.0 and 29.1 mm, CL01, st 153, set 147, 43°33′N 59°04′W, August 31, 1977, 2035 h, neuston, surface.

Myctophum affine is a "tropical" species which is commonly expatriated northward by the Gulf Stream (Nafpaktitis et al. 1977). It is frequently captured in nighttime neuston samples. Two other specimens have been recorded from the Canadian Atlantic (Leim and Scott 1966).

ORDER LOPHIIFORMES

Family OGCOCEPHALIDAE

Genus and species unknown (batfish) — HML — H2619, 1 specimen, 4.1 mm SL, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, 0225 h, IKMT, 144 m.

The specimen superficially resembles a ceratioid larva but the presence of pelvic fins eliminates all ceratioids

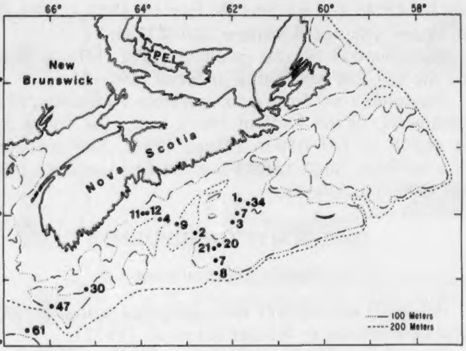

FIG. 4. Scotian Shelf showing location and number of individuals of adult red hake caught during cruise LH03, July 1978.

except *Caulophryne* (Bertelsen 1951). However, *Caulophryne* spp. have 3–4 pelvic fin rays and 13–19 anal fin rays, whereas our specimen has 5 pelvic fin rays plus what looks like a short spine closely applied to the outer ray, 4 anal fin rays, 4+ dorsal fin rays, 15–16 pectoral fin rays, 9 caudal fin rays and 5 branchiostegal rays. The Antennariidae are likewise eliminated by the low anal fin ray count and high pectoral fin ray count (Schultz 1964). There are a pair of melanophores on each hemisphere of the brain and a double row of about seven melanophores on the nape. The meristics agree with the Ogcocephalidae (Jordan and Evermann 1896) but not with the only locally known ogcocephalid, *Dibranchus atlanticus* (Leim and Scott 1966). In view of the large number of subtropical and tropical expatriates reported herein, we cannot eliminate more southerly species from consideration.

Family ANTENNARIIDAE

Antennarius sp. (frogfish) — HML — H1255, 1 specimen, 11.7 mm, CC01, st 36, set 47, 43°56′N 58°30′W, February 24, 1977, 0710 h, IKMT, 234 m.

The specimen is a kanazawaichthys — type prejuvenile with a pair of enlarged bony plates on the head. Otherwise it is similar to the ceratioid and ogcocephalid larvae. The dorsal fin has three spines, the first, which is slightly longer than the second, has a slightly enlarged tip or "lure." There are 13 soft dorsal fin rays, 13 pectoral rays, and 8 anal rays, all of which appear to be branched. Two species, *A. ocellatus* and *A. radiosus*, fit the observed meristics but the presence of a long first dorsal spine and branched pectoral fin rays are contradictory on the basis of adult morphology (Schultz 1957).

The genus is found in shallow subtropical waters.

ORDER GADIFORMES

Family GADIDAE

Urophycis chuss (Walbaum) (red hake) — 277 adult specimens from 16 trawl stations (Fig. 4), *Lady Hammond* LH03, July 1978.

The senior author participated in *Lady Hammond* cruise LH03 on the Scotian Shelf from July 13–19, 1978 and was able to check the identity of all *Urophycis* that were caught. Of 358 *Urophycis* caught, 277 (77%) were red hake, *U. chuss*. The rest were white hake, *U. tenuis*. Identifications were based on the number of epibranchial gill rakers (Musick 1973). Usually, red hake could be superficially separated from white hake by their relatively larger scales and generally smaller size. In addition to these specimens, numerous larvae and juveniles of *Urophycis* spp. have been collected during the first years of SSIP. Most of the juveniles are *U. chuss*. Their distribution in the ichthyoplankton is now under study by D. Methven (HML).

Musick (1967, 1973) presented information which implied that the northern range of *U. chuss* could, for fisheries purposes, be assumed to be Georges Bank. In spite of his later contribution (Musick 1973), which provides a simple means for identification, there is still much confusion about the species of *Urophycis* on the Scotian Shelf. A perusal of recent literature indicates that most Scotian Shelf *Urophycis* collected by Canadian vessels are *U. tenuis* while those collected by Soviet and Cuban vessels are *U. chuss*. The present data raise serious questions about the validity of fisheries data based upon the assumption of a single species fishery. Annual variation in the relative contribution of each species to the fishery is unknown and requires long-term study.

Family MERLUCCIIDAE

Merluccius albidus (Mitchill) (offshore hake) — HML — H460, 1 specimen 5 mm, P182, st 36, set 105, 43°58′N 58°35′W, May 16, 1977, 1740 h, bongo, 230 m. HML — H443, 2 specimens 6 and 8 mm, P182, st 88, set 69, 43°02′N 62°03′W, May 12, 1977, 1731 h, bongo, 102 m. HML — H2954, 1 specimen 9 mm, CL01, st 108, set 60, 43°18′N 63°30′W, August 16, 1977, 1225 h, bongo, 137 m. HML — H2957, 21 specimens 3–8 mm, CL01, st 105, set 63, 42°50′N 63°02′W, August 16, 1977, 1850 h, bongo, 115 m. HML — H2958, 1 specimen 4.5 mm, CL01, st 90, set 64, 42°48′N 62°40′W, August 16, 1977, 2115 h, bongo, 274 m. HML — H2966, 98 specimens 3–10 mm, CL01, st 104, set 72, 43°06′N 62°58′W, August 17, 1977, 1650 h, bongo, 110 m. HML — H2967, 30 specimens 3–11 mm, CL01, st 103, set 73, 43°16′N 63°00′W, August 17, 1977, 1900 h, bongo, 91 m. HML — H2973, 2 specimens 2.5 and 4 mm, CL01, st 95, set 79, 43°48′N 62°28′W, August 18, 1977, 0545 h, bongo, 123 m. HML — H3047, 9 specimens 2–3 mm, CL01, st 71, set 154, 43°30′N 60°58′W, September 1, 1977, 1825 h, bongo, 46 m. HML — H3061, 27 specimens 2–3 mm, CL01, st 69, set 9, 44°00′N 61°00′W, August 9, 1977, 1910 h, meter net, surface. HML — H3211, 1 specimen 4 mm, CL01, st 108, set 60, 43°18′N 63°30′W, August 16, 1977, 1225 h, bongo, 137 m. HML — H3212, 2 specimens 3 and 4 mm, CL01, st 105, set 63,

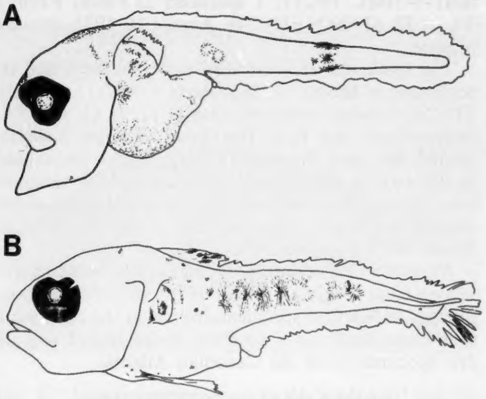

FIG. 5. *Merluccius albidus*. A, HML-H460, 4.9 mm SL, left lateral view; B, HML-H2967, 9.0 mm SL, left lateral view.

42°50′N 63°02′W, August 16, 1977, 1850 h, bongo, 115 m. HML — H3214, 36 specimens, 3–6 mm, CL01, st 104, set 72, 43°06′N 62°58′W, August 17, 1977, 1650 h, bongo, 110 m. HML — H3215, 42 specimens 3–8 mm, CL01, st 103, set 73, 43°16′N 63°00′W, August 17, 1977, 1900 h, bongo, 91 m. HML — uncatalogued, 1 specimen 236 mm, LH03, set 18, 42°46.8′N 63°58.1′W, July 15, 1978, 0210 h, 50 m Engel otter trawl, 249–272 m.

Very early larvae of *M. albidus* were described by Marak (1967). They differ from larvae of *M. bilinearis* in the greater snout pigmentation and lack of a caudal spot. From the series on hand it is apparent that *M. albidus* is also a deeper bodied larva than *M. bilinearis* and that it develops denser pigmentation on the pectoral and pelvic fins as well as a series of large midlateral melanophores (Fig. 5). Adults are apparently regularly caught near the outer edge of the Scotian Shelf but were previously misidentified as *M. bilinearis*. In addition to differences in numbers of gill rakers and lateral line scales (Ginsburg 1954), the two species of *Merluccius* can be quickly rough sorted by the absence of cheek pigmentation in *M. bilinearis* (Fig. 6A) and the relatively broader snout and blockier head of *M. albidus* (Fig. 6B).

Bigelow and Schroeder (1955) reported that they did not catch any *M. albidus* north of Georges Bank during a 1953 survey. As with the discrepancy about the *U. chuss* literature (above), we cannot determine whether the different observations are due to sampling error or reflect annual environmental changes.

Family MORIDAE

Physiculus fulvus (Bean) — NMC 78-279, 1 specimen 40.0 mm, CC01, st 72, set 64, 43°16′N 60°58′W, March 3, 1977, 0735 h, neuston, surface.

The specimen, a juvenile (Fig. 7A), agrees with

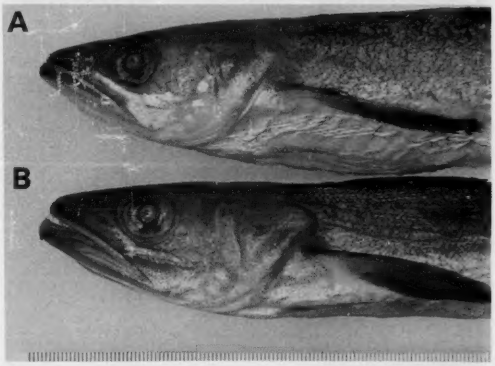

FIG. 6. A, *Merluccius bilinearis*, HML — uncatalogued, 238 mm SL, left lateral view of head; B, *Merluccius albidus*, HML — uncatalogued, 237 mm SL, left lateral view of head.

the description in Goode and Bean (1896). Selected meristics were D_1 9, D_2 54, A 61, P_2 7 (outer two rays elongate).

Physiculus fulvus is an engybenthic continental slope species reported as far north as 35°N (Goode and Bean 1896). Our specimen apparently represents the first epipelagic capture, a northern range record for the species and the first specimen from the Canadian Atlantic.

ORDER OPHIDIIFORMES

Family CARAPIDAE

Echiodon sp. (undescribed pearlfish) — HML — H927, 1 specimen 3.8 mm HL, CC01, st 50, set 59, 43°36′N 59°30′W, March 2, 1977, 1110 h, neuston, surface.

The specimen was included in the description of *Echiodon* sp. larvae by Olney and Markle (1979).

Adults of this undescribed species are only known from a few specimens from the Gulf of Mexico (Olney and Markle 1979). In more recent cruises we have numerous multiple captures of larval *Echiodon*. Our specimen is the northern range record for the species and the first specimen from the Canadian Atlantic.

Family OPHIDIIDAE

Ophidion selenops (Robins and Böhlke) (mooneye cusk-eel) — HML — H2619, 3 specimens, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, 0225 h, IKMT, 144 m. HML — H2620, 1 specimen, CL01, st 137, set 37, 42°09′N 65°26′W, August 14, 1977, 0640 h, IKMT, 79 m. HML — H2930, 3 specimens, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, 0225 h, bongo, 119 m.

These larvae were identified to either of the genera *Ophidion* or *Lepophidium* using the keys and descriptions in Cohen and Nielsen (1978) and Jordan and

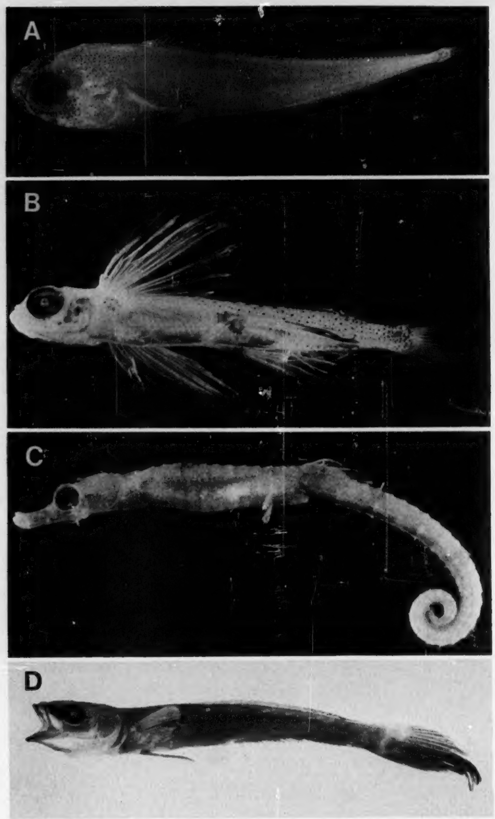

FIG. 7. A, *Physiculus fulvus*, NMC 78-279, 40.0 mm SL, left lateral view; B, *Hirundichthys affinis*, NMC 78-277, 22.8 mm SL, left lateral view; C, *Amphelikturus dendriticus*, NMC 78-283, 39.3 mm SL, left lateral view; D, *Rachycentron canadum*, NMC 78-275, 42.7 mm SL, left lateral view.

Evermann (1896). Specific identification was made possible using meristics of a cleared and stained specimen, H2930, which were D 138, A 124 and vertebrae 16 + 63 = 79, which fit only *O. selenops* (C. Powell personal communication; Robins and Böhlke 1959).

Adults of this species have been found from the Gulf of Mexico (Dry Tortugas) and the Florida Current off the mideastern coast of Florida (Robins and Böhlke 1959). Our larvae represent northern range records and the first specimens from the Canadian Atlantic.

ORDER ATHERINIFORMES

Family EXOCOETIDAE

Hirundichthys affinis (Gunther) (fourwing flying fish) — NMC 78-277, 1 specimen 22.8 mm, P170, st 32, set 32, 43°00′N 62°02′W, August 16, 1976, neuston, surface.

The specimen was identified using the keys and descriptions in Breder (1938), Parin (1961), and Fahay (1975). Selected meristics were D 11, A 11, P_1 17 (1 unbranched), and P_2 6. The dorsal fin origin is slightly behind the anal fin origin. The pectoral fin extends to the anus; a chin barbel is absent; the preopercular-mandibular canal does not communicate with the supraorbital; the snout length is 0.8 mm and the orbit diameter is 2.1 mm (Fig. 7B).

Hirundichthys affinis is a continental shelf species known from Virginia (Breder 1938) to northern Brazil (Briggs 1958). Our specimen, from near the continental shelf-slope break, is a northern range record and the first specimen from the Canadian Atlantic.

ORDER GASTEROSTEIFORMES

Family SYNGNATHIDAE

Amphelikturus dentriticus (Barbour) (pipehorse) — HML — H2776, 31.5 mm and NMC 78-283, 39.3 mm, CL01, st 138, set 38, 42°19′N 65°30′W, August 14, 1977, 0840 h, neuston, surface.

The specimens have a prehensile tail with a vestigial caudal fin (Fig. 7C), a head that is slightly inclined to the body axis, a pair of ornamental dermal appendages before the anus, a raised dorsal fin base, only 16 dorsal fin rays situated over 1 trunk and 4 tail rings, and a total of 14–15 trunk rings and 38–39 tail rings (Herald 1959, Böhlke and Chaplin 1968). Neither specimen has a brood pouch.

Dawson (1972) and Fahay (1975) report a total of 27 known specimens from the Bermudas and Bahamas and from off New Jersey, Maryland, North Carolina, Florida, Dominican Republic, and Mississippi. Dawson's three specimens from off Mississippi were juveniles, 29.1–31.7 mm, caught in July and August and he noted that most offshore Gulf of Mexico syngnathids were juveniles and were often associated with floating *Sargassum* (Dawson 1972). Similarly, our specimens were also caught in summer, were in a sample containing a large quantity of floating brown algae, and were juveniles. Our specimens are a northern range record for the species and the first specimens from the Canadian Atlantic.

ORDER SCORPAENIFORMES

Family SCORPAENIDAE

Type A (probably *Scorpaena*) — HML — H930, 1 specimen 12.8 mm, CC01, st 53, set 61, 43°30′N 59°56′W, March 2, 1977, 1620 h, neuston, surface. HML — H2812, 1 specimen 11.0 mm, CL01, st 102, set 74, 43°31′N 63°00′W, 2115 h, August 17, 1977, neuston, surface. HML — 113Z599, 1 specimen 10.5 mm, P170, st 18, 42°36′N 64°32′W, August 14, 1976, neuston, surface.

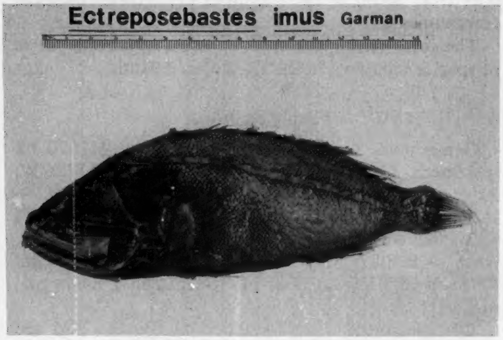

FIG. 8. *Ectreposebastes imus*, ROM 35142, 165 mm SL, left lateral view.

Type B (probably *Pontinus*) — HML — 113Z688, 1 specimen 12.7 mm, P170, st 31, 43°02′N 62°30′W, August 16, 1976, IKMT, 175 m.

Tentative identifications were aided by Eschmeyer (1969) and Moser et al. (1977).

Ectreposebastes imus Garman — ROM 35142, 1 specimen 165.0 mm, *P. J. Lawrence* cruise, 42°54′N 62°30′W (Nova Scotian Shelf), May 31, 1971, otter trawl, 475.5 m (260 fm).

The specimen (Fig. 8) was identified by Dr B. B. Collette. The systematics and distribution of *E. imus* were reviewed by Eschmeyer and Collette (1966), Eschmeyer (1969), and Collette and Uyeno (1972). Peritoneum dusky with dark spots anteriorly, pale posteriorly. Selected meristics: D XII 9, A III 6, P_1 (left) 19.

Eschmeyer (1969) reported two specimens taken off St. Augustine, Florida, at Oregon Station 5233, 29°54.5′N 80°10′W. These were the first records for the Atlantic coastal waters of the United States. The present record thus extends the western Atlantic range considerably northward.

Family TRIGLIDAE

Peristedion miniatum Goode (armoured searobin) — ROM 35141, 1 specimen 179.0 mm, *A. T. Cameron* cruise 250, set 36, 42°35′35″N 64°32′30″W (SSE of Cape Sable, N.S.), July 17, 1976, otter trawl, 195.7 m (107 fm).

Peristedion miniatum ranges from southwestern Georges Bank southward along the Atlantic seaboard of the United States to the northern Gulf of Mexico (Briggs 1958).

Occasional specimens are reportedly caught by commercial trawlers on the Scotian Shelf but positive identification of specimens is seldom possible. Records north of Cape Cod are rare, hence this specimen represents a northern range record and the first specimen from the Canadian Atlantic.

Prionotus carolinus (Linnaeus) (northern searobin) — HML — H2619, 1 specimen 9.6 mm, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, 0225 h, IKMT, 145 m.

Identification is based on Ginsburg (1950) and Teague (1961). Meristics (D X, 13; A 11; and gill rakers, including incompletely formed nubs, on lower limb of first arch 10) agree with *P. carolinus*.

Kuntz and Radcliffe (1917) noted that development was fast in *Prionotus*. It would therefore seem likely that only the more northerly species of *Prionotus* (*carolinus* and *evolans*) could be expected as expatriates in the Canadian Atlantic. Leim and Scott (1966) noted that *P. carolinus* was uncommon north of Cape Cod and that all Canadian Atlantic records had been from the Bay of Fundy. The present specimen was caught well offshore on the Scotian Shelf and would appear to be an obvious southern expatriate.

ORDER DACTYLOPTERIFORMES

Family DACTYLOPTERIDAE

Dactylopterus volitans (Linnaeus) (flying gurnard) — NMC 78-281, 1 specimen 43.5 mm, CL01, st 119, set 24, 43°03′N 64°02′W, August 13, 1977, 0200 h, neuston, surface.

Leim and Scott (1966) mention three previous Canadian Atlantic records, all of which they considered open to doubt. *Dactylopterus volitans* is common between North Carolina and Brazil and present as a stray to Massachusetts (Leim and Scott 1966; Monod 1973). Our specimen represents a northern range record for the species and the first specimen from the Canadian Atlantic.

ORDER PERCIFORMES

Family SERRANIDAE

Anthias (?) — HML — 113Z673, 1 specimen 21.5 mm, P170, st 16, 42°07′N 65°34′W, August 14, 1976, IKMT, 435 m.

This identification is tentative.

Family APOGONIDAE

Apogon pseudomaculatus Longley (two-spot cardinalfish) — HML — H3091, 1 specimen 17 mm, CL01, st 140, set 40, 42°45′N 65°28′W, August 14, 1977, 1205 h, meter net, surface.

This identification is tentative and based on Fraser (1972) and Böhlke and Chaplin (1968).

Family BRANCHIOSTEGIDAE

Lopholatilus chamaeleonticeps (Goode and Bean) (tilefish) — NMC 78-286, 1 specimen 490 mm, LH03, set 25, 43°00.1′N 62°12.4′W, July 15, 1978, 50 m Engel trawl, 122–135 m.

Leim and Scott (1966) report four records from the Canadian Atlantic, none of the specimens of which are apparently extant. It is known from Banquereau, La Have, Emerald and Roseway Banks and is most abundant along a very restricted depth (120–200 m) and temperature (about 15°C) range (Dooley 1978).

Family RACHYCENTRIDAE

Rachycentron canadum (Linnaeus) (cobia) — NMC 78-275, 1 specimen 42.7 mm, P170, st 33, 43°15′N 62°08′W, August 16, 1976, meter net, surface.

The specimen agrees with Dawson's (1971) description of juvenile *R. canadum* (Fig. 7D).

Rachycentron canadum is circumtropical in distribution and reported from Massachusetts to Argentina in the western Atlantic (Briggs 1958). Although young specimens (<250 mm SL) are rare, the information available to Dawson (1971) suggested that larger juveniles (>45 mm) in the Gulf of Mexico may tend to move from offshore to inshore localities. The presence of a 42.7-mm specimen east of Emerald Bank on the Scotian Shelf suggests long distance transport of this species by the Gulf Stream. Our specimen is a northern range record and the first specimen from the Canadian Atlantic.

Family SCIAENIDAE

Micropogonias undulatus (Linnaeus) (Atlantic croaker) — HML — H2619, 1 specimen 6.2 mm, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, 0225 h, IKMT, 144 m.

The specimen fits the description of *M. undulatus* by Hildebrand and Cable (1930) and Fruge and Truesdale (1978).

The Atlantic croaker ranges from Cape Cod possibly to Argentina (Chao 1978). Our specimen represents a northern range record and a Canadian Atlantic record.

Family LABRIDAE

Genus and species unknown. HML — H2619, 14 specimens, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, 0225 h, IKMT, 144 m. HML — H2620, 1 specimen, CL01, st 137, set 37, 42°09′N 65°26′W, August 14, 1977, 0640 h, IKMT, 79 m. HML — H2774, 3 specimens, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, 0225 h, neuston, surface. HML — H2930, 4 specimens, CL01, st 136, set 36, 42°23′N 65°01′W, August 14, 1977, 0245 h, bongo, 119 m. HML — H2960, 1 specimen, CL01, st 88, set 66, 43°02′N 62°04′W, August 17, 1977, 0200 h, bongo, 99 m. HML — H3087, 3 specimens, CL01, st 136, set 36, 42°23′N 65°01′W, August 14, 1977, 0245 h, meter net, surface. HML — H3088, 3 specimens, st 137, set 37, 42°10′N 65°25′W, August 14, 1977, 0610 h, meter net, surface.

The above specimens were identified by Dr H. Powles, DFO, Quebec. These specimens are now under study by Powles, and include species known as adults only from south of the Carolinas (H. Powles personal communication).

The specimens apparently represent expatriate larvae of species unknown in the Canadian Atlantic.

Family SCARIDAE

Genus and species unknown. HML — H2620, 2 specimens, CL01, st 137, set 37, 42°09′N 65°26′W, August 14, 1977, 0640 h, IKMT, 79 m. HML — H2774, 3 specimens, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, 0225 h, neuston, surface. HML — H3087, 3 specimens, CL01, st 136, set 36, 42°23′N 65°01′W, August 14, 1977, 0245 h, meter net, surface.

The specimens were identified by Powles and are now under study.

The family is tropical or subtropical and previously unknown from the Canadian Atlantic.

Family CALLIONYMIDAE

Callionymus pauciradiatus (Gill) (spotted dragonet) — HML — H3087, 1 specimen ca. 3.2 mm,, CL01, st 136, set 36, 42°23′N 65°01′W, August 14, 1977, 0245 h, meter net, surface.

The specimen was identified with the unpublished keys and notes of Olney and Sedberry.

Adults are known from the Bahamas, Florida, and Cuba (Böhlke and Chaplin 1968). Larvae of *Callionymus* are apparently regularly dispersed northward by the Gulf Stream (J. Olney and G. Sedberry personal communication) and in more recent cruises we have two examples of the congener, *C. bairdi*. Our specimens represent the northern range records and the first specimens from the Canadian Atlantic.

Family GOBIIDAE

Genus and species unknown. HML — 113Z673, 1 specimen 8.0 mm, P170, st 16, 42°07′N 65°34′W, August 14, 1976, IKMT, 435 m. HML — H2619, 2 specimens 9.2 and 11.9 mm, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, 0225 h, IKMT, 144 m. HML — H2774, 3 specimens, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, neuston, surface. HML — H3088, 7 specimens, CL01, st 137, set 37, 42°10′N 65°25′W, August 14, 1977, meter net, surface.

There are two types of gobies present in these collections. Additional examples of both types have been found in more recent cruises.

Most gobies are subtropical or tropical. These specimens represent the first capture of the family in the Canadian Atlantic.

ORDER PLEURONECTIFORMES

Family BOTHIDAE

Citharichthys arctifrons (Goode) (Gulf Stream

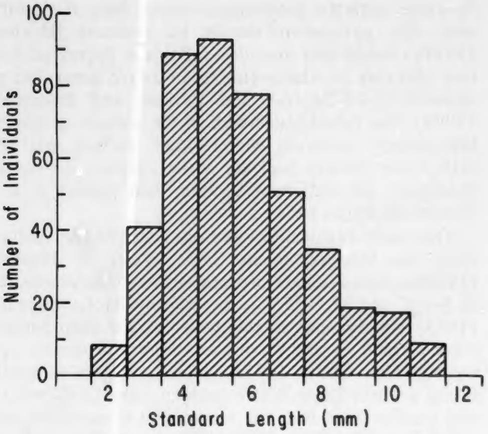

FIG. 9. Length frequency distribution of *Citharichthys arctifrons* from cruise CL01, August 1977.

flounder) — NMC 78-287, 2 specimens 79.3 and 105 mm, LH03, set 43, 43°26.5′N 62°16.2′W, July 17, 1978, 2115 h, 50 m otter trawl, 104 m. HML — H1388, 1 specimen 34.5 mm, CC01, st 97, set 9, 44°00′N 62°28′W, February 16, 1977, 1913 h, meter net, surface. HML — numerous (49) collections of larvae (2–11 mm, Fig. 10) from *Canso Light*, CL01, August 1977.

Identifications were based on the keys and descriptions of Gutherz and Blackman (1970) and Parr (1931) and the larval description of Richardson and Joseph (1973). On the Scotian Shelf, larvae of *C. arctifrons* are most similar to larval *Limanda ferruginea* and *Pseudopleuronectes americanus*. However, the elongate first dorsal fin rays, well developed swimbladder, precocious dentition, and overall pigmentation readily separate *C. arctifrons* larvae.

Citharichthys arctifrons was previously known from Georges Bank to northeastern Gulf of Mexico (Briggs 1958; Gutherz 1967; Colton and Byron 1977). The largest NMC specimen is a ripe or ripening female. In addition, we have seen numerous adult specimens collected over the past several years from the Scotian Shelf. This, together with the length frequency distribution of larvae from August 1977 (Fig. 9), suggests that a viable spawning population exists on the Scotian Shelf. The geographic distribution of larvae (Fig. 10) is relatively restricted, not indicative of a contiguous southern population nor of Gulf Stream dispersal (e.g. *E. eurystole*, whose distribution follows the shelf-slope break) and, therefore, also indicates the presence of a discrete population.

The discovery of what appears to be a large spawning population of *C. arctifrons* on the Scotian Shelf requires comment. As with the discrepancies about *Merluccius albidus* and *Urophycis chuss* (above), we have no firm data base to determine if the different observations are due to sampling error or annual environmental changes. Since most research trawling on the Scotian Shelf is with large commercial-sized trawls which probably undersample smaller fishes, it is possible that this small species (less than 190 mm, Bigelow and Schroeder 1953) and perhaps small populations of other species have been easily missed.

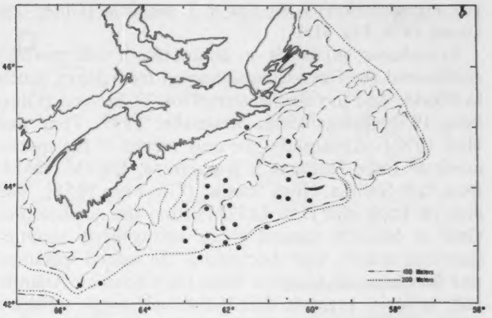

FIG. 10. Scotian Shelf showing geographic distribution of *Citharichthys arctifrons* from cruise CL01, August 1977.

Syacium sp. — HML — H2619, 2 specimens 7.7 and 7.9 mm, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, 0225 h, IKMT, 144 m. HML — H2620, 1 specimen 12.5 mm, CL01, st 137, set 37, 42°09′N 65°26′W, August 14, 1977, 0640 h, IKMT, 79 m. HML — H2776, 1 specimen 7.7 mm, CL01, st 138, set 38, 42°19′N 65°30′W, August 14, 1977, 0840 h, neuston, surface.

Bothus sp. — HML — numerous collections, from Scotian Shelf, mostly east of Browns Bank and west of Emerald Bank (distribution included in Fig. 10).

Identifications of *Syacium* and *Bothus* are based on Gutherz (1967, 1970) and Aboussouan (1968). The *Syacium* are either *S. micrurum* or *S. papillosum* and the *Bothus* either *B. ocellatus* or *B. robinsi* (see Gutherz 1967).

Larvae of both *Syacium* and *Bothus* have previously been reported from the Canadian Atlantic (Dannevig 1919, Gutherz 1970; Evseenko 1976), though generally from further offshore.

Family CYNOGLOSSIDAE

Symphurus minor (Ginsburg) (large scale tonguefish) — HML — H2774, 1 specimen 7.3 mm, CL01, st 136, set 36, 42°21′N 65°01′W, August 14, 1977, 0225 h, neuston, surface.

Identification was confirmed using the key and descriptions in Ginsburg (1951), Topp and Hoff (1972), and Miller and Jorgenson (1973). Our specimen was cleared and stained and its low fin ray counts and number of vertebrae (D 75, A 59, vertebrae 41) easily distinguish this species from other cynoglossids. The general appearance of this larva (overall shape, trailing gut, pigmentation) is similar to *S. plagiusa* (Olney and Grant 1976, Fig. 3D).

Symphurus minor is a diminutive (<80 mm SL) continental shelf cynoglossid known from Nova Scotia to Florida and the northeastern Gulf of Mexico (Ginsburg 1951; Briggs 1958; Struhsaker 1969; Topp and Hoff 1972). Apparently, the only record of the species north of Cape Hatteras is a paratype USNM 92614, from "off Halifax, Nova Scotia" (Ginsburg 1951). The data of Topp and Hoff (1972), from the northeastern Gulf of Mexico, suggest a late spring–early summer spawning season. Our specimen is the second specimen and first larva of *S. minor* from the Canadian Atlantic and, at least, suggests that individuals might exist on the Scotian Shelf through recruitment from the south.

ORDER TETRAODONTIFORMES

Family Ostraciontidae

Lactophrys triqueter (Linnaeus) (smooth trunkfish) — HML — H2763, 1 specimen 9.4 mm, CL01, st 120, set 25, 42°47′N 64°01′W, August 13, 1977, 0402 h, neuston, surface.

The specimen was identified using the keys and descriptions in Jordan and Evermann (1896) and Böhlke and Chaplin (1968). Our specimen represents a northern range record and the first Canadian Atlantic record.

Physiographic and Hydrographic Data

In the middle portion of the western Scotian Shelf is a large, deep (greater than 125 m) area which has been referred to as the Scotian Gulf (Hachey 1937b) and includes Emerald and La Have basins. Roseway, La Have, Sambro, and Emerald banks form elevations over this area and a deep channel between La Have Bank and Emerald Bank extends the Scotian Gulf southward to the edge of the continental slope (Hachey 1937b, 1953).

The hydrography at any point on the Scotian Shelf is a complicated function of depth, location, season, and atmospheric conditions (McLellan 1954a). In summer there is normally a three-layered stratification of the water column with the coldest area at any depth in the northeastern sector and the warmest in the Scotian Gulf (Bigelow 1927; McLellan et al. 1953). The relatively low salinity water of the eastern Scotian Shelf is derived from surface water of the Gulf of St. Lawrence which floods the eastern shelf to Banquereau and cold bottom water with Labrador Current characteristics which can be found to the slope off Sable Island Bank (McLellan 1954a, b; Sutcliffe et al. 1976).

One aspect of vertical stratification is Ekman drift of the surface water caused by prevailing winds and consequent upwelling of offshore water in the Scotian Gulf. In summer the predominant winds are from the southwest and thus there should be movement of surface water normal to the coastline with onshore replacement by deeper bottom water (Hachey 1937a). In winter with the predominant winds from the northeast, this circulation should be reversed. Hachey (1937a) found corroboration for this in decreased bottom salinities in winter (less than 34‰) compared to summer (34.0–34.9‰) and Barinov and Bryantsev (1972) also found a decrease in the volume of warm, high salinity water in winter. Late summer and fall drift bottle returns indicate a net cyclonic (counterclockwise) circulation of Scotian Shelf surface waters (Trites and Banks 1958).

The warm, high salinity bottom water of the Scotian Gulf was referred to as Slope Water by Hachey (1937b) with temperature and salinity characteristics of 5–8°C and 33.5–35.0‰, respectively. McLellan et al. (1953) simply refer to this water as the deep coastal layer formed by the mixing of slope and deeper upwelled water. Gatien (1976), looking in greater detail, found a warm Slope Water zone near the Gulf Stream and another zone near the continental slope which she called Labrador Slope Water. The warm Slope Water moved eastward with the Gulf Stream while the Labrador Slope Water moved westward. Further she found Labrador Slope Water below 100 m with σ_t values near 27.5 and temperatures from 8–10°C. Recently, Houghton et al. (1978) demonstrated how cross-shelf mixing dilutes Slope Water with subsurface water from Cabot Strait.

In the Scotian Gulf, historical hydrographic data suggest that the warm, saline bottom water (Labrador Slope Water in part, see below) is a persistent feature of the Scotian Gulf showing little seasonal or systematic change. For example, in winter 1952, the bottom water temperatures of the Scotian Gulf were greater than 9°C and in the coldest years they apparently do not fall much below 7°C (McLellan 1954a).

In contrast to the apparent stable conditions of Slope Water, the unstable, wavelike northern boundary of the Gulf Stream contributes spatially and temporally unstable systems. These are the anticyclonic (clockwise) warm-core Gulf Stream eddies or rings (Saunders 1971). These are not always easy to identify from surveys of the type discussed here, but can be approximately matched to our data using satellite infrared photographs.

In order to characterize the hydrography of the Scotian Shelf during the period when most of the fishes under consideration were captured, surface and bottom temperature, salinity, and density were contoured for July 1977 (Fig. 11). These data come from a groundfish survey during *A. T. Cameron* cruises A265 and A266. As the literature indicates, the bottom water of the Scotian Gulf is warm (>9°C), of high salinity (>35‰) and dense (>27.0). In July 1977, the highest values for each within the Scotian Gulf were 10.8°C, 35.46‰, and 27.4. This indicates Labrador Slope Water which is being diluted as suggested by Houghton et al. (1978). The surface temperature, salinity, and density also indicate encroachment of warm, high salinity water in the vicinity of the Scotian Gulf (Fig. 11). The sur-

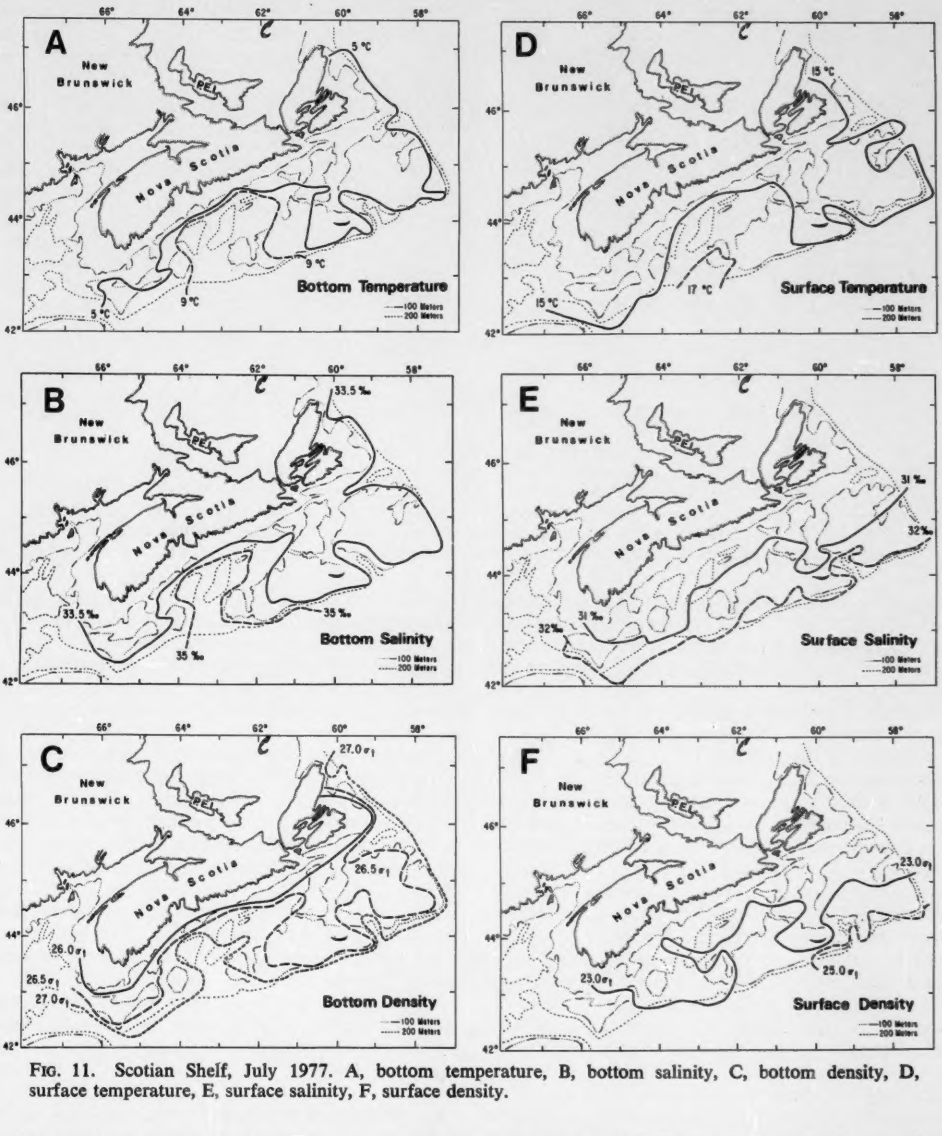
A
New Brunswick
PEI
Nova Scotia
5 °C
9 °C
9 °C
5 °C
Bottom Temperature
100 Meters
200 Meters
D
New Brunswick
PEI
Nova Scotia
15 °C
17 °C
15 °C
Surface Temperature
100 Meters
200 Meters
B
New Brunswick
PEI
Nova Scotia
33.5 ‰
33.5 ‰
35 ‰
35 ‰
Bottom Salinity
100 Meters
200 Meters
E
New Brunswick
PEI
Nova Scotia
31 ‰
32 ‰
31 ‰
32 ‰
Surface Salinity
100 Meters
200 Meters
C
New Brunswick
PEI
Nova Scotia
27.0 σt
26.5 σt
26.0 σt
26.5 σt
27.0 σt
Bottom Density
100 Meters
200 Meters
F
New Brunswick
PEI
Nova Scotia
23.0 σt
25.0 σt
23.0 σt
Surface Density
100 Meters
200 Meters
66°
64°
62°
60°
58°
46°
44°
42°

FIG. 11. Scotian Shelf, July 1977. A, bottom temperature, B, bottom salinity, C, bottom density, D, surface temperature, E, surface salinity, F, surface density.

face isobars indicate the potential for a small-scale cyclonic (counterclockwise) eddy in the surface water over the Scotian Gulf (Smith et al. 1978).

Discussion and Conclusions

A total of 42 kinds of fishes are reported as new or rare from the Canadian Atlantic. They can be approximately grouped into two categories: viable populations of the Canadian Atlantic and expatriated or transient individuals.

Two of the three species reported above which appear to have viable populations appear most abundant in or near the Scotian Gulf. The distributions of larval Gulf Stream flounder (Fig. 9) and adult red hake (Fig. 4) are approximately congruent with the

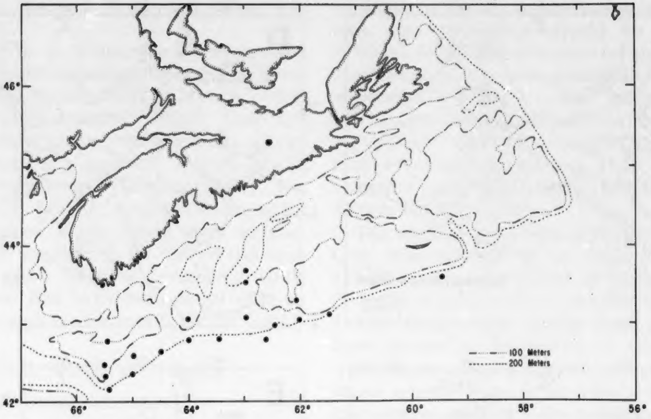

FIG. 12. Scotian Shelf showing geographic distribution of Engraulidae, Synodontidae, Chlorophthalmidae, Ogcocephalidae, Antennariidae, Carapidae, Ophidiidae, Exocoetidae, Syngnathidae, Scorpaenidae, Triglidae, Dactylopteridae, Serranidae, Apogonidae, Branchiostegidae, Rachycentridae, Sciaenidae, Labridae, Scaridae, Callionymidae, Gobiidae, *Syacium*, *Bothus*, Cynoglossidae, and Ostraciontidae reported in text.

physiography of this deep basin. The third species which appears to have a viable population in the Canadian Atlantic is the offshore hake. It is an upper slope species which has frequently been misidentified in the past.

There are several questions which relate to the long-term stability and recruitment of Gulf Stream flounder and red hake. If the adults are living near their lower thermal limit, periodic "cold years" could cause local extinctions which might lead to subsequent recruitment of adults from refugia on the continental slope or of larvae from further south. If the populations are self-sustaining as Fig. 10 indicates for Gulf Stream flounder and as unpublished data indicate for red hake (D. Methven (HML) unpublished data), the mechanism of larval entrainment on the Scotian Shelf is open to question. Although our evidence is inconclusive, a cyclonic eddy or temperature preference could contribute to the observed distribution patterns of larvae.

Most of the new records of fishes are of subtropical forms which have been dispersed northward by the Gulf Stream. Their distribution (Fig. 12) is approximately congruent with the edge of the continental slope and appears to be in the area of mixing associated with Slope Water. Satellite photographs indicate that several of the stations from cruise CL01 (136, 137) may have been near the wave-like northern edge of the Gulf Stream or a warm-core Gulf Stream eddy.

The uniformity of their combined distributions contrasts with the different life histories and adult distributions of these fishes. For example, it is quite possible that juvenile silver anchovies and snakefish, and larval pearlfish and bothids are normal residents of the warmer waters above the Scotian continental slope. Pearlfish and bothid larvae are well known long distance drifters (Futch 1977; Olney and Markle 1979), but the prevailing currents would appear to expatriate these specimens from the adult habitat. The snakefish and red lizardfish, on the other hand, are known from the eastern Atlantic (Anderson et al. 1966; Nielsen 1973) and presumably could be recruited to these populations. All of these species might also be recruited to the parent populations if they possess an ethological mechanism to take advantage of the southward drift of Labrador Slope Water or warm-core Gulf Stream eddies. However, there is no evidence that this might actually occur.

The large number of subtropical expatriates raises the question of their ultimate fate. Sale (1978) considers the optimal life history strategy for a coral reef fish to include widespread dispersal of its larvae so that new habitats can be exploited as they appear. Long distance dispersal of fish larvae by the Gulf Stream (Fahay and Obenchain 1978; Olney and Markle 1979) and amphi-Atlantic distributions of some tropical organisms (Scheltema 1968; Briggs 1970) support this idea. Inherent in this "lottery" strategy is a huge loss to expatriation. Most of the specimens that reach the Canadian Atlantic probably perish; however, some may survive to adulthood, either in the Canadian Atlantic or in the eastern Atlantic through transatlantic dispersal.

We have no evidence that any of the expatriates might survive as nonreproducing adults on the Scotian Shelf in a situation similar to the warmwater chaetognaths of the Gulf of Maine (Bigelow 1926) or the ceratioids (Bertelsen 1951) and myctophids (O'Day and Nafpaktitis 1967; Zurbrigg and Scott 1972) of the boreal North Atlantic. That adults of warmer water species can survive in the Canadian Atlantic is documented by the tautog, *Tautoga onitis*, fishery of Eel Brook Lake, Nova Scotia, which produced 2000–3000 large tautogs for anglers in 1957 and 1958 (Leim and Scott 1966) and then collapsed. The tautogs were apparently recruited to Eel Brook Lake through a mechanism other than larval dispersal since it is a strictly inshore species and we have never found their larvae in SSIP cruises. However, their presence inshore and the presence offshore of adult tilefish, longnose greeneye, red hake, *E. imus*, armoured searobin, Gulf Stream flounder, and large-scale tonguefish suggest that a continuum of marginal habitats is available on the Scotian Shelf to some warmwater species.

The complex hydrography of the Scotian Shelf allows at least temporary exploitation by some subtropical fishes which reach the area. The tongue of warm water which transects the shelf (Fig. 11) may act as a summer corridor to the bays of Nova Scotia. A spectrum of warmwater fishes is found on the Scotian Shelf: from the "lottery" larvae dispersed by the Gulf Stream, to species that can survive temporarily, to species which appear to be able to complete their life cycle within its confines.

The existence of eastern Atlantic populations of some of the species reported herein raises the possibility of transatlantic dispersal. Scheltema (1968) points out that west–east dispersal by the North Atlantic Drift is available only to eurythermal forms and that the Equatorial Undercurrent is the only available current for stenothermal forms. The existence of a dispersal mechanism does not ensure viable dispersal (Futch 1977), so that without knowledge of larval thermal tolerances we cannot predict which species might have a good chance of making the west to east crossing. Evidence from known adult distributions suggests that less than 10% of the expatriates reported herein might be successful.

The nature of the North Atlantic gyre is such that Templeman (1962) has also invoked this mechanism to explain the presence of a specimen of the pelagic eastern Atlantic puffer, *Lagocephalus lagocephalus*, off Newfoundland. The unstable, wavelike western boundary of the Gulf Stream off Nova Scotia plus the ichthyoplankton data clearly indicate a substantial influence of Gulf Stream water on the Scotian Shelf. This influence is both hydrographic and faunistic but its temporal variation is unknown. Likewise, the ecological effects of Gulf Stream water and its associated fauna on resident species is unknown.

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Séparation des populations de hareng de l'Atlantique (*Clupea harengus harengus*) de l'estuaire du Saint-Laurent et de la péninsule gaspésienne

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CÔTÉ, G., P. LAMOUREUX, J. BOULVA ET G. LACROIX. 1980. Séparation des populations de hareng de l'Atlantique (*Clupea harengus harengus*) de l'estuaire du Saint-Laurent et de la péninsule gaspésienne. Can. J. Fish. Aquat. Sci. 37: 66–71.

L'examen de caractères morphométriques et méristiques de harengs de l'Atlantique (*Clupea harengus harengus*) capturés durant le frai, le long de la côte gaspésienne et dans l'estuaire du Saint-Laurent, a permis d'établir qu'au moins trois populations distinctes sont exploitées par la pêche dirigée vers cette espèce, dans cette région. La première fréquente surtout l'estuaire du Saint-Laurent et se reproduit au printemps, dans la région de l'Isle-Verte; elle est caractérisée par une croissance très lente. Les deux autres se retrouvent autour de la péninsule gaspésienne; l'une se reproduit au printemps et l'autre, à l'automne.

Mots clés: hareng de l'Atlantique, estuaire du Saint-Laurent, péninsule gaspésienne, caractères morphométriques, caractères méristiques

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Examination of morphometric and meristic characteristics of Atlantic herring (*Clupea harengus harengus*) caught during spawning along the Gaspé coast and the St. Lawrence Estuary lead to the conclusion of the existence of at least three herring populations in that area. The first one occurs in the St. Lawrence Estuary, spawns in the spring and is characterized by smaller length-at-age values than the two other populations which are comprised respectively of spring-spawners and autumn-spawners that are fished off the Gaspé peninsula.

Key words: Atlantic herring, St. Lawrence Estuary, Gaspé peninsula, morphometric characteristics, meristic characteristics

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DES travaux visant à vérifier s'il existe plusieurs populations de hareng de l'Atlantique (*Clupea harengus harengus*) (Jean 1956; Day 1957a; Parsons et Hodder 1971; Messieh et Tibbo 1971) ont démontré la présence de deux grandes catégories, l'une caractérisée par une reproduction printanière, l'autre par une reproduction automnale. Jean (1956) et Day (1957a) ont étudié plus particulièrement la région qui nous intéresse: l'estuaire du Saint-Laurent, fréquenté par des poissons qui fraient au printemps, et le pourtour de la péninsule gaspésienne, où l'on retrouve à la fois du hareng qui fraie au printemps et du hareng qui fraie à l'automne.

Jean (1956) a conclu de ses travaux que le hareng qui se reproduit au printemps, dit « hareng de printemps », et celui qui se reproduit à l'automne, dit « hareng d'automne », ne sont pas deux populations homogènes. Il peut en effet arriver que des poissons éclos au printemps se reproduisent à l'automne et vice versa. Par ailleurs, d'autres auteurs, tels que Day (1957a), Parsons et Hodder (1971) et Messieh et Tibbo (1971) concluent différemment. Selon eux, le hareng de printemps et le hareng d'automne constituent deux populations bien distinctes. Day (1957b) a même avancé l'hypothèse que le hareng de printemps du nord du golfe du Saint-Laurent pouvait être composé de plus d'une population.

Notre objectif était de vérifier, par l'examen de poissons capturés pendant le frai, les hypothèses émises antérieurement, et notamment de voir s'il n'y a pas, en

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plus des stocks déja connus, d'autres populations de hareng dans la région.

Matériel et Méthodes

Nous avons prélevé des échantillons de hareng frayant à l'Isle-Verte, dans l'estuaire du Saint-Laurent, en mai et juin 1977, et à divers endroits de la péninsule gaspésienne (Saint-Yvon, Ste-Thérèse-de-Gaspé, Carleton), entre mai et octobre de la même année (Fig. 1). La figure 2 présente une ventilation, par localité, des 1100 individus en état de reproduction. Les poissons furent capturés dans des trappes à fascines, à l'Isle-Verte, et dans des filets maillants dont la maille étirée variait de 5,7 à 7,0 cm, dans les trois autres endroits.

Nous avons mesuré la longueur totale du poisson, du bout de la mâchoire inférieure jusqu'à l'extrémité du lobe le plus étiré de la nageoire caudale. Nous avons également déterminé l'âge, en comptant, sur les otolithes, les zones opaques représentant la croissance estivale. Ces déterminations étaient faites en lumière directe, aux grossissements de 12× et 25× d'une loupe binoculaire. Afin d'obtenir une meilleure résolution, les otolithes étaient submergées dans l'alcool éthylique à 98%, et ensuite lues selon la méthode recommandée par Hunt *et al.* (1973). Ces données de longueur et d'âge ont permis d'estimer les taux de croissance. Nous nous sommes par ailleurs intéressés à quatre caractères méristiques: le nombre de rayons de la nageoire dorsale et pectorale gauche, le nombre de branchicténies du limbe inférieur du premier arc branchial gauche et finalement le nombre de scutelles osseuses entre les nageoires pelviennes et l'anus. Ces mesures furent effectuées à la loupe binoculaire, en lumière directe et à un grossissement de 6×.

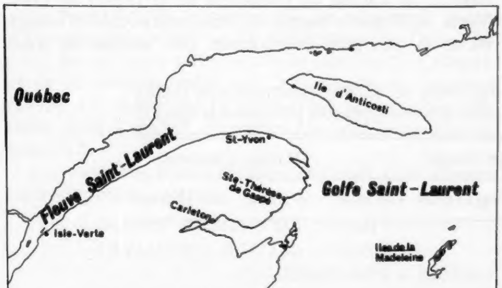

FIG. 1. Les régions d'échantillonnage.

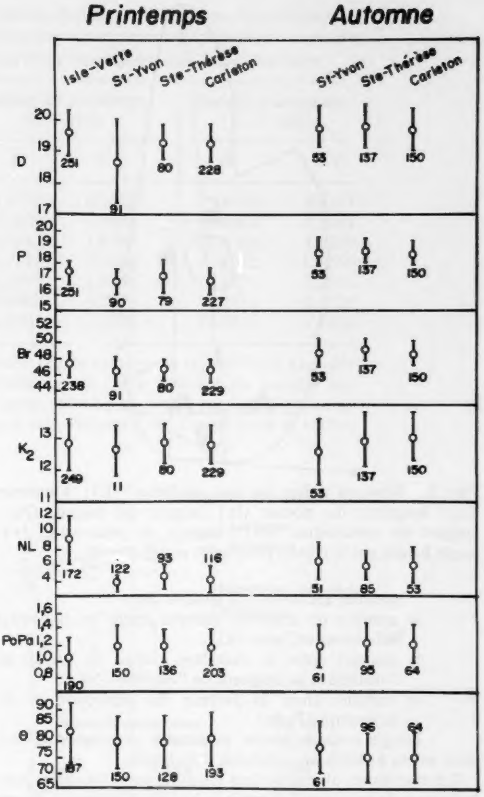

FIG. 2. Moyennes et écarts-types des variables analysées sur le hareng de printemps et le hareng d'automne des diverses régions d'échantillonnage: les rayons de la nageoire dorsale (D); les rayons de la nageoire pectorale gauche (P); le nombre de branchicténies du limbe inférieur du premier arc branchial gauche (Br); le nombre de scutelles osseuses entre les nageoires pelviennes et l'anus (K_2); le rapport entre le diamètre moyen du noyau de l'otolithe et la longueur de l'otolithe (NL); le rapport entre la largeur du postrostre et du pararostre (PoPa); l'angle entre le rostre, postrostre et pararostre (θ).

Enfin, nous avons fait une analyse morphométrique des otolithes, à partir de dessins réalisés à l'aide d'une loupe binoculaire munie d'un tube à dessin, en lumière directe et en utilisant un grossissement de 25×. Les otolithes étaient alors immergées dans de l'alcool à 98%. Nous n'avons utilisé que l'otolithe droite, selon la recommandation de Messieh (1972), et mesuré sur chacune la longueur comprise entre le rostre et l'extrémité du pararostre, l'angle (θ) formé par les lignes rejoignant le rostre au postrostre et ce dernier au pararostre, le rapport entre la largeur du postrostre et du pararostre (PoPa) et finalement la longueur (lo) et largeur (la) du noyau de l'otolithe afin d'établir son diamètre moyen (Fig. 3). NL, soit le diamètre moyen du noyau de l'otolithe exprimé en fonction de la longueur des otolithes, est obtenu par la formule suivante:

$$\mathrm{NL} = \frac{100\,\mathrm{D}}{\mathrm{L}}$$

où D est le diamètre moyen du noyau de l'otolithe et L est la longueur de l'otolithe.

Après avoir recueilli les sept variables mentionnées, soit:

les rayons de la nageoire dorsale (D),

les rayons de la nageoire pectorale gauche (P),

le nombre de branchicténies du limbe inférieur du

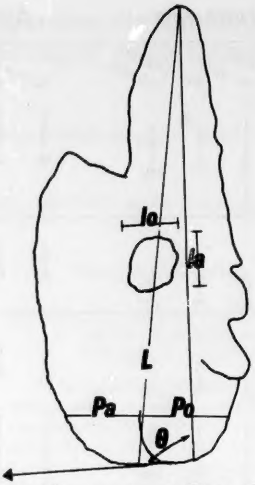

FIG. 3. Mesures faites sur les otolithes. (L): longueur; (lo): longueur du noyau; (la) largeur du noyau; (Pa): largeur du pararostre; (Po): largeur du postrostre; (θ): angle formé par le rostre, postrostre et pararostre.

premier arc branchial gauche (Br),

le nombre de scutelles osseuses entre les nageoires pelviennes et l'anus (K_2),

le rapport entre le diamètre moyen du noyau de l'otolithe et la longueur de l'otolithe (NL),

le rapport entre la largeur du postrostre et du pararostre (PoPa),

l'angle entre le rostre, postrostre et pararostre (θ);

nous avons procédé aux analyses statistiques.

Les moyennes obtenues dans les différentes localités, pour le hareng de printemps et pour le hareng d'automne, furent soumises au test de Student-Newman Keuls (SNK) (Sokal et Rohlf 1969). Nous avons ensuite pris parmi ces poissons un sous-échantillon au hasard et avons effectué une analyse de fonction discriminante (Nie *et al.* 1975) en vue de définir les populations de hareng au moyen d'équations linéaires.

Résultats

Selon l'analyse statistique pratiquée sur les variables retenues (Fig. 2), le hareng de printemps de l'Isle-Verte est très différent de celui des différentes localités de la péninsule gaspésienne. Les différences dans les moyennes sont significatives dans les cas d'au moins cinq des sept variables (Tableau 1). Par comparaison, le hareng de printemps de la péninsule gaspésienne présente très peu de différences significatives d'une localité à l'autre (Saint-Yvon, Sainte-Thérèse-de-Gaspé, Carleton) à l'égard des mêmes variables. La même observation s'applique au hareng d'automne, envisagé au plan géographique. Pour chacune des localités, il y a cependant plusieurs différences significatives entre le hareng de printemps et le hareng d'automne de la péninsule gaspésienne (Tableau 1).

L'examen des courbes de croissance du type von Bertalanffy ajustées aux données de longueur–âge, pour le hareng de printemps de l'Isle-Verte et pour le hareng de printemps et d'automne de la péninsule gaspésienne (Fig. 4), suggère une différence dans la croissance de ces trois groupes de poissons. Il faut noter cependant que ces courbes ne sont valables que pour les poissons de 3 ans et plus, car nos données, peu nombreuses, n'ont pas permis de faire les estimations nécessaires, pour les âges inférieurs. Les paramètres de ces courbes de croissance (Fig. 4) ont été estimés par la méthode de Beverton (1954). Nous constatons que le hareng de printemps de la région de l'Isle-Verte atteint une longueur par âge inférieure à celle du hareng des deux autres groupes. Nous constatons également que le hareng de printemps de la péninsule gaspésienne a une croissance plus lente que le hareng d'automne de cette même région. Des tests de Student-Newman-Keuls (SNK) démontrèrent une différence significative à $\alpha = 0{,}05$, pour les valeurs longueur–âge entre les trois groupes. Il est à noter que la différence entre la croissance du hareng de printemps et le hareng d'automne avait été observée antérieurement pour le hareng du golfe du Saint-Laurent (Messieh et Tibbo 1971; Parsons 1972).

Plusieurs indices concordent donc pour suggérer l'existence, dans la région, de trois populations de hareng: le hareng de printemps de la région de l'Isle-Verte, ainsi que le hareng de printemps et celui d'automne de la péninsule gaspésienne. Une analyse de fonc-

TABLEAU 1. Nombre de différences significatives (tests de Student-Newman-Keuls (SNK) pour $\alpha = 0{,}05$) pour les 7 variables dont les moyennes et écarts-types sont présentés à la figure 2.

	Hareng de printemps				Hareng d'automne	
	Isle-Verte	St-Yvon	Ste-Thérèse	Carleton	St-Yvon	Ste-Thérèse
Hareng de printemps						
St-Yvon	6					
Ste-Thérèse	6	2				
Carleton	6	2	2			
Hareng d'automne						
St-Yvon	5	5	5	5		
Ste-Thérèse	5	5	5	5	2	
Carleton	5	5	5	5	2	1

TABLEAU 2. Moyennes et écarts-types des variables utilisées pour l'analyse discriminante.

	Isle-Verte		St-Yvon, Ste-Thérèse-de-Gaspé, Carleton			
	Hareng de printemps (*n* = 78)		Hareng de printemps (*n* = 194)		Hareng d'automne (*n* = 155)	
Variables[a]	$\bar{X}$	E.T.	$\bar{X}$	E.T.	$\bar{X}$	E.T.
D	19,5091	0,7908	19,1707	0,7055	19,8296	0,6162
P	17,6545	0,7258	17,0853	0,9154	18,8064	0,8395
Br	47,4545	1,5616	46,7683	1,6597	48,8306	1,6368
K_2	12,8545	0,9113	12,7317	0,7008	13,0322	0,8554
NL	8,6090	3,3554	4,2597	1,9799	5,8291	2,2991
PoPa	1,0380	0,1945	1,1901	0,2071	1,2516	0,2620
θ	83,6364	8,1911	80,8902	7,3081	76,0645	7,7449

[a] (D), le nombre de rayons de la nageoire dorsale. (P), le nombre de rayons de la nageoire pectorale de gauche. (Br), le nombre de branchicténies du limbe inférieur du premier arc branchial gauche. (K_2), le nombre de scutelles osseuses entre les nageoires pelviennes et l'anus. (PoPa), le rapport entre la largeur du postrostre et du pararostre. (θ), l'angle entre le rostre, postrostre et pararostre.

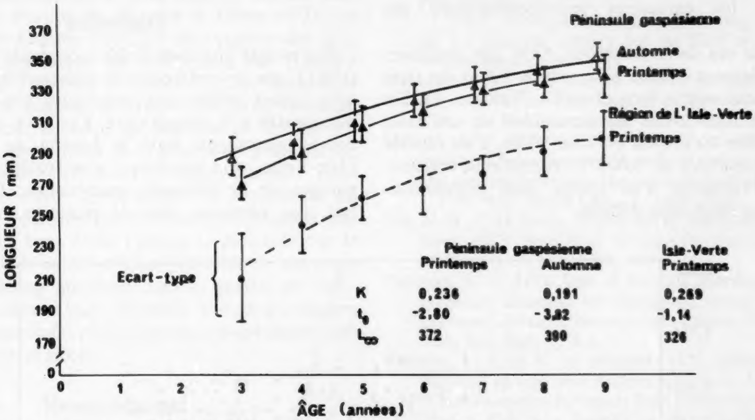

FIG. 4. Courbes de croissance du type von Bertalanffy ajustées aux données de longueur–âge.

tion discriminante a permis de les séparer à partir d'équations linéaires, après vérification de l'homogénéité des variances au moyen de la fonction de Kullback et de la multinormalité par la méthode de Dagnelie (1975). Les moyennes et écarts-types des variables utilisées pour l'analyse discriminante sont présentés au tableau 2.

Les fonctions d'identification obtenues pour séparer les trois groupes sont:

$$Y_1 = 24{,}48535 - 0{,}261191\,D - 0{,}51005\,P - 0{,}21454\,Br - 0{,}7651\,K_2 - 0{,}00522\,NL - 0{,}59400\,PoPa + 0{,}02306\,\theta$$

$$Y_2 = 7{,}58626 - 0{,}04356\,D - 0{,}001665\,P - 0{,}03786\,Br - 0{,}07949\,K_2 - 0{,}30250\,NL + 0{,}76435\,PoPa - 0{,}03425\,\theta$$

ou Y_1 et Y_2 représentent respectivement, la première et la seconde variable canonique.

A partir des coefficients standardisés (Tableau 3), on remarque que les caractères suivants discriminent le plus dans la première fonction: le nombre de rayons de la nageoire pectorale gauche (P), le nombre de branchicténies du limbe inférieur du premier arc branchial gauche (Br) ainsi que l'angle (θ) entre le rostre, le postrostre et le pararostre de l'otolithe. Pour la seconde fonction, le rapport NL suivi de l'angle (θ) et du rapport PoPa discriminent davantage. Sur la carte territoriale du pointage discriminant (Fig. 5), la première fonction est représentée par l'axe des abcisses et la seconde, par l'axe des ordonnées. On constate, sur cette carte, que le hareng d'automne se sépare des deux groupes de hareng de printemps, surtout selon l'axe des abcisses; c'est donc dire que ce sont les caractères méristiques qui le différencient. Les deux groupes de hareng de printemps se divisent surtout selon l'axe des ordonnées, qui obtient son pouvoir discriminant

TABLEAU 3. Coefficients standardisés des fonctions discriminantes.

Variables[a]	Fonction n° 1	Fonction n° 2
D	−0,18842	−0,03133
P	−0,58828	−0,01920
Br	−0,39358	−0,06946
K_2	−0,06461	−0,06712
NL	−0,01524	−0,88383
PoPa	−0,14212	0,18288
θ	0,19229	−0,28557

[a](D), le nombre de rayons de la nageoire dorsale. (P), le nombre de rayons de la nageoire pectorale de gauche. (Br), le nombre de branchicténies du limbe inférieur du premier arc branchial de gauche. (K_2), le nombre de scutelles osseuses entre les nageoires pelviennes et l'anus. (NL), le rapport entre le diamètre du noyau de l'otolithe et la longueur de l'otolithe. (PoPa), le rapport entre la largeur du postrostre et du pararostre. (θ), l'angle entre le rostre, postrostre et pararostre.

surtout par les caractères morphométriques des otolithes.

A partir de ces deux fonctions, 83% des poissons, jugés préalablement comme appartenant à l'un des trois groupes, se sont avérés bien classifiés (Tableau 4). De plus, la séparation entre les centroïdes de ces trois groupes, vérifiée au moyen du λ de Wilks, s'est révélée significative pour un α de 0,001. Ceci confirme vraisemblablement l'existence d'au moins trois populations de hareng dans notre zone d'étude.

TABLEAU 4. Pourcentage de classification des poissons appartenant aux diverses populations de hareng de notre zone d'étude, obtenu à partir de l'analyse discriminante.

	% des poissons classifiés par groupe		
	Groupe 1	Groupe 2	Groupe 3
Groupe 1 Hareng de printemps Région de l'Isle-Verte	73,1	23,1	3,8
Groupe 2 Hareng de printemps Région de St-Yvon, Ste-Thérèse-de-Gaspé et Carleton	6,7	85,6	7,7
Groupe 3 Hareng d'automne Régions de St-Yvon, Ste-Thérèse-de-Gaspé et Carleton	6,5	4,5	89,0

Discussion

Il n'est pas invraisemblable, comme le proposait Jean (1967), que les différences morphométriques et méristiques soient reliées aux conditions océanographiques, notamment à la température. Les eaux de l'estuaire du Saint-Laurent, où fraie le hareng de printemps de l'Isle-Verte, sont nettement plus froides que celles des parages de la péninsule gaspésienne. Blaxter (1958) fait, par exemple, état de plusieurs travaux expéri-

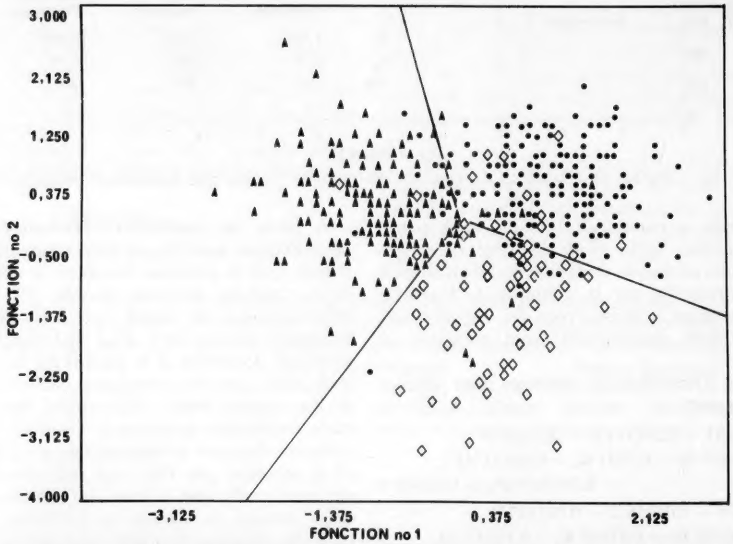

FIG. 5. Carte territoriale du pointage discriminant. ▲ = Hareng d'automne de la péninsule gaspésienne; ● = Hareng de printemps de la péninsule gaspésienne; ◇ = Hareng de printemps de la région de l'Isle-Verte.

mentaux montrant des liens entre les basses températures d'un milieu d'élevage de larves de hareng et les valeurs plus faibles obtenues dans les caractéristiques méristiques.

Il est également intéressant de noter qu'Able (1978) a évalué le taux de croissance de larves de hareng capturées dans l'estuaire du Saint-Laurent à 0,15 mm/d et 0,17 mm/d, selon l'année d'échantillonnage. Ces taux sont fortement inférieurs à ceux mentionnés par Ware et Henriksen (1978) de 0,5 mm/d pour le hareng de printemps des Iles-de-la-Madeleine. Ware et Henriksen (1978) établissent à 190 jours la période de croissance des larves dans l'année de leur éclosion et à 40 mm la taille avant de se métamorphoser. Si ces valeurs s'appliquent au hareng de l'Estuaire, cela impliquerait que le hareng de printemps de cette région ne se métamorphoserait pas durant la première année suivant l'éclosion, ce qui pourrait expliquer les faibles tailles obtenues par les adultes.

Les différences entre le hareng de printemps et celui d'automne dans le golfe du Saint-Laurent étaient bien établies par les travaux de Messieh et Tibbo (1971) et Parsons (1972). D'autre part, par une analyse des taux de croissance et numérations vertébrales, Day (1957b) avait été amené à émettre l'hypothèse d'une distinction possible entre le hareng de l'Isle-Verte dans l'estuaire du Saint-Laurent, et celui de Matane et Rivière-au-Renard, sur la partie nord de la péninsule gaspésienne, mais sans pouvoir vraiment l'étayer, comme nous l'avons fait ici. Cette confirmation de l'existence, au sein du hareng de printemps, de deux composantes distinctes, constitue sans doute l'aspect le plus inédit et le plus intéressant de ce travail. La première de ces composantes, le hareng qui fraie dans la région de l'Isle-Verte, est maintenant bien identifiée. Il n'est pas encore certain que la seconde, plus nettement gaspésienne, soit constituée d'un seul stock.

Remerciements

Nous désirons remercier madame Céline Trudeau-Simard, ainsi que messieurs Jean Dubé et Jean Lauzier pour leur aide technique. Nous voulons également remercier le Dr Louis Legendre pour ses conseils au niveau du traitement mathématique de nos données, et le Dr S. N. Messieh, pour son aide continuelle tout au long de ce projet.

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Oxygen Depletion in Lake Erie: Has There Been Any Change?

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CHARLTON, M. N. 1980. Oxygen depletion in Lake Erie: Has there been any change? Can. J. Fish. Aquat. Sci. 37: 72–81.

A new analysis of hypolimnetic oxygen in Central Lake Erie indicates that historic increases in the apparent depletion were not as great as formerly believed. The differences that did occur were mostly related to variations in hypolimnion thickness. Changes, if any, in the oxygen depletion rate due to eutrophication are as yet too small to be recognized. Present-day oxygen depletion rates, when corrected for the relatively high temperatures in Lake Erie, are within the range thought to be indicative of mesotrophy in small lakes. The general level of oxygen depletion observed in the Central Basin of Lake Erie is expected on the basis of morphology alone.

Key words: Lake Erie, oxygen, hypolimnion, oxygen depletion, trend

CHARLTON, M. N. 1980. Oxygen depletion in Lake Erie: Has there been any change? Can. J. Fish. Aquat. Sci. 37: 72–81.

Une nouvelle analyse de l'oxygène hypolimnétique dans le bassin central du lac Erié indique que les augmentations historiques de l'épuisement apparent n'étaient pas aussi prononcées qu'on l'avait cru. Les différences qui se sont en fait produites étaient liées surtout aux variations d'épaisseur de l'hypolimnion. Les changements, s'il en est, de taux d'épuisement d'oxygène par eutrophisation sont encore trop faibles pour être identifiables. Les taux actuels d'épuisement d'oxygène, lorsque corrigés pour tenir compte des températures relativement élevées du lac Erié, se situent dans la gamme que l'on considère indicatrice de mésotrophie dans des petits lacs. On peut s'attendre, d'après la seule morphologie du lac, au niveau général d'épuisement d'oxygène observé dans le bassin central du lac Erié.

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INCREASES in the rate of depletion of hypolimnetic oxygen in Lake Erie have been attributed to cultural eutrophication occurring since the 1920s (Dobson and Gilbertson 1971). Although the depletion rate might indicate some difference in trophic status between lakes, very few lakes have been studied long enough to determine the amount and cause of variability in oxygen depletion rates. Thus, if two different measurements of oxygen depletion rate were obtained some years apart in a lake, testing whether a difference was caused by an external factor, e.g. nutrient loading, or whether a difference was significant at all, would be difficult. In order to relate trends in oxygen depletion and cultural eutrophication, compensation for coincidental changes in physical factors may be necessary. As an example, consider a lake which has become subjected to heating, sewage disposal, and damming; while net effects may be determined by an extended before–after study, assigning a proportion of change to any one use would be difficult without actual measurements of changes in temperature, nutrient concentration, and water depth. In addition, one would hope for comparable weather patterns during the two parts of the study.

Hypolimnetic oxygen depletion is caused by decreased downward transport of oxygen across the thermocline, the presence of oxidizable material, and biological and chemical processes. Many small temperate lakes, completely unaffected by human activity, have anoxic hypolimnia by the end of summer stratification, illustrating that some degree of deoxygenation is normal and not necessarily a sign of excessive enrichment. An unenriched lake will have a background average depletion rate with year-to-year or perhaps decade-to-decade variation. Some measure of the short- and long-term variability of oxygen depletion is necessary to elucidate the meaning of differences between years. By determining and measuring factors which cause variation in oxygen depletion rates, an assessment of these effects on apparent trends may be made. The purpose of this paper is to determine the scope for interpretation in historic Lake Erie oxygen data and examine the effects of factors which may cause variation in the oxygen depletion rate.

Oxygen Depletion Rates

The apparent trend to increasing depletion rates in Lake Erie in the period 1929–70 has been discussed by Dobson and Gilbertson (1971) who stated that some selection of data was necessary in the analysis. Carr (1962) and Beeton (1963) indicated that early studies, in 1929 and 1948–53, might have included

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TABLE 1. Variation of hypolimnion oxygen concentration (mg/L) in Central Lake Erie during 1929. (* Denotes values which are the same as or within 1.1 mg/L of near surface oxygen.)

Station	June 17 (weakly stratified)		July 12 (within 12°C isotherm)		August 17 (within 14°C isotherm)
30	8.5				7.9*
35	9.5		9.3*		8.3*
40	8.9		7.5		7.1*
41	8.7		6.8		4.8
42	9.5		7.0		5.6
45	9.3		8.0		4.4
33	10.0		7.1		
34	10.1		9.3*		
39	9.3		7.2		
46	8.1				
44	9.2		7.0		
43	8.7		7.0		
Mean:	9.2		7.6		6.4
Monthly change:		1.9		1.0	
Mean of nonsurface values:	9.2		7.2		4.9
Monthly change:		2.4		1.9	
Mean of nonsurface values within 14°C isotherm:	9.2		7.3		4.9
Monthly change:		2.3		2.0	

inappropriate data due to sampling problems and less than representative station patterns. Because of the importance of the early rates in the determination of the trend, I reexamined the data to determine whether a variety of interpretations were possible.

There were great differences in the quantity and quality of data available. Oxygen depletion rates calculated from early data, 1929, 1948–53, were typically based on 1–4 stations, whereas the later rates, 1959–1963, 1967–1970, were based on 15–33 stations. On the other hand, sampling was more frequent in 1948–1953 than in other years.

1929

In 1929, depths recorded on repeat visits to the same station often differed by several metres and some part of the metalimnion may have been included in hypolimnion samples. The few temperature profiles available in 1929 (Fish 1960) indicate that the lake was weakly stratified in June, but strongly stratified in July and August, with hypolimnion temperatures below 12 and 14°C, respectively. Table 1 shows the pertinent data and some possible interpretations. Temperature profiles and isopleth maps of near bottom temperature (Fish 1960), indicate that the usable data in July are within the 12°C isotherm. When the lake was sampled in August only half (6) of the July stations were within the 14°C isotherm, which marked the upper boundary of the hypolimnion. Three of these six data are similar to surface oxygen concentrations and indicate that these samples do not represent hypolimnion oxygen. Of the hypolimnion oxygen depletion rates in Table 1, the June–July calculations are doubtful because stratification may not have persisted in June. The first two July–August calculations are based on inappropriate data and, therefore, also rejected. A reasonable monthly depletion rate, based on the 1929 data, appears to be 2.0 mg/L; this is 25% higher than that reported by Dobson and Gilbertson (1971). Due to the small number of sampling dates and stations, little confidence can be attached to any estimate of the oxygen depletion rate in 1929. Assuming that half of the important August values were for metalimnion waters, the three data used to calculate the rate may represent a mix of hypolimnion and metalimnion water (Carr 1962) and the actual depletion rate may have been higher than I have calculated. Extrapolating these data for another month results in oxygen concentrations as low as 2–3 mg/L in mid-September. While the exact rate is undeterminable, significant oxygen depletion occurred in 1929.

1948–1953

Oxygen data for 1948–53 were collected by the University of Western Ontario and published by Powers et al. (1960). Most of these data were collected at stations (No. 1 to 6) beginning near Erieau and extending midway on a line to Cleveland. Other, less frequent, data were from stations (No. 14 to 23) on a

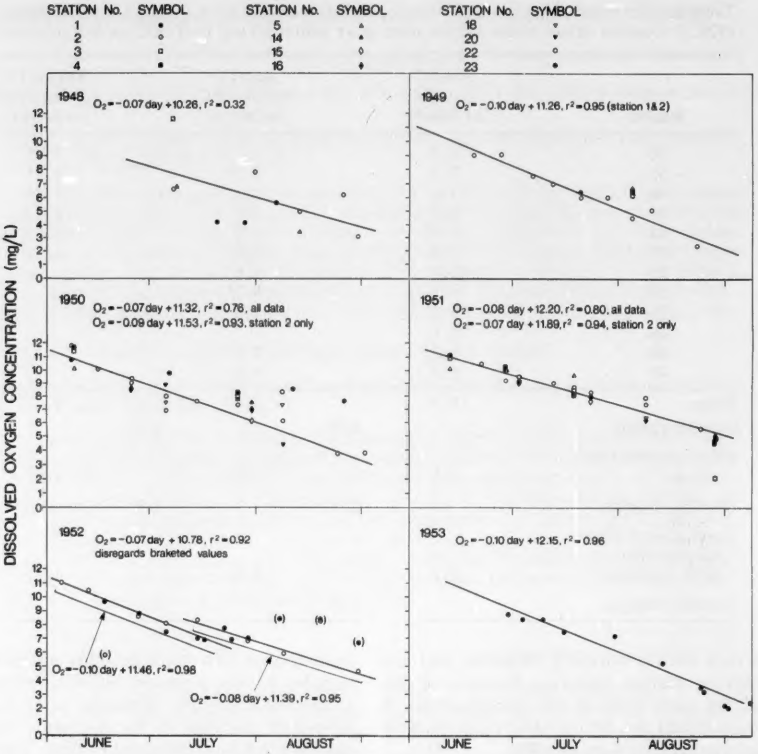

FIG. 1. Oxygen depletion in the hypolimnion of central Lake Erie 1948–53. Points represent individual observations. Data are from Powers et al. (1960).

line from Point Pelee to Long Point. I have used oxygen values reported as "bottom" at stations that were thermally stratified. Oxygen data reported from the hypolimnion at arbitrary depths above the "bottom" were not used as these were often intermediate between surface and "bottom" values.

The data for 1948–53 and calculated regression lines are shown in graphical form on Fig. 1. In general, oxygen concentrations declined in a regular, linear fashion during the summer with two notable exceptions. The 1948 data are sporadic and scattered; as the regression is not significant at the 5% level, I do not consider the data to be useful. The 1952 data are complicated by a very low value in June, four unexplicably high values in August, and a sort of discontinuity of concentration and, to some degree, rate of decline in mid-July. If all these data are used, a low slope and poor correlation are found, which probably misrepresent the depletion rate. Such a discontinuity in slope and oxygen concentration at a small number of stations (2) may be caused by a weather event and/or water mass movement. If this was the case, data before and after the discontinuity need not be treated as points in the same trend, but may be used to calculate two slopes. Figure 1 (1952) shows a clear trend developed in June and another devloped in July–August; even the slope of the four high August data is similar to that developed by the main data. Consequently, two slopes are reported which are both somewhat higher than the slope derived from a regression of all but the odd data. This approach, while speculative, seems preferable to lumping the data or discarding them.

For the years 1949, 1950, 1951, and 1953, station 1 or 2 was sampled frequently and several other stations were sporadically represented. Regression values calculated for both the single station alone and including all data are shown in Fig. 1. Slightly better correlations were obtained with the single station data.

Some of the oxygen depletion rates calculated from the University of Western Ontario data for 1948–53 differ from those reported previously by Dobson and Gilbertson (1971). The 1948 data do not appear suit-

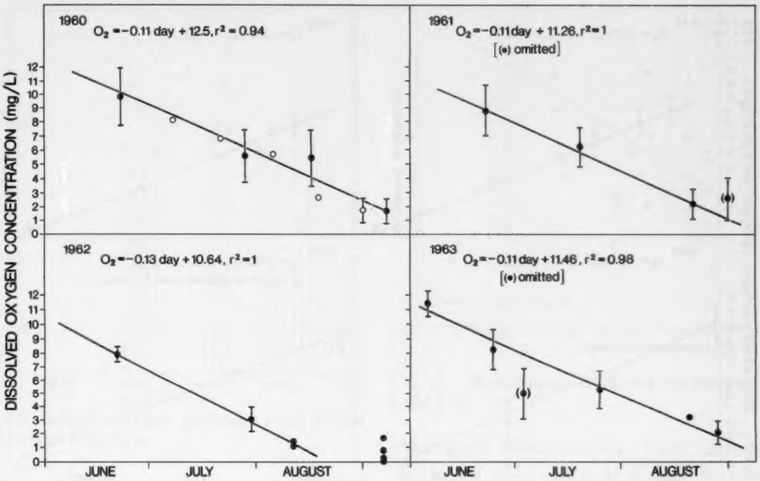

FIG. 2. Oxygen depletion in the hypolimnion of central Lake Erie 1960–63. Points and regression represent cruise means ±1 SD. Data are from the Great Lakes Institute (1964, 1965) and Rodgers (1962, 1963). Additional data in 1960 are from Beeton (1963) (open circles).

able for the calculation of a depletion rate, but my analysis of the 1951 data yields a depletion rate similar to the findings of Dobson and Gilbertson (1971). The remaining monthly oxygen depletion rates are all higher than previously reported; some are equivalent to 3 mg/L, which may be the critical rate for the occurrence of anoxia given sufficient duration of stratification. In general, restricting the analysis to data which represented only the stratified period at regularly sampled stations (Charlton 1979) resulted in the differences between the present results and those of Dobson and Gilbertson (1971).

1960–63 and 1967–70

After 1953, oxygen data were collected in 1960–63 by the Great Lakes Institute (GLI), and in 1967–70 by the Canada Centre for Inland Waters. In general, these data were collected at a greater number of stations more evenly distributed in the lake than before, and are supported by a large number of reversing thermometer and bathythermograph recordings. Due to better sampling, features such as incursion of colder East Basin hypolimnion water and lack of stratification at very shallow stations were revealed. Only rarely were station patterns repeated exactly, and on some cruises there was a high concentration of stations close to Cleveland.

For the purpose of oxygen depletion rate calculation, some data selection was again necessary. Due to the great variety of station location and distribution, each datum was checked for misprints and to ensure that the water was stratified. I used near bottom oxygen data at stratified stations that were over 15 m deep and showed no evidence of incursion of colder East Basin water. In addition, to avoid a bias in the calculations, I arbitrarily chose only one of the many stations that were close to Cleveland on some cruises.

The mean (±1 SD) hypolimnion oxygen concentrations for each cruise were plotted at the mid point of each cruise and the best straight line found by linear regression. Results are shown in Fig. 2 and 3. The 1960 cruises were augmented by data from a station near Wheatley (Beeton 1963). The daily oxygen depletion rate of 0.10 mg/L in 1970 is slightly lower than 0.11 mg/L reported by Burns (1976a) because no correction was made for oxygen added from the metalimnion to the hypolimnion. This type of calculation was omitted because it depends on the determination of whole basin quantities and is, therefore, inconsistent with the limitations of the earlier data.

Since some of the earlier data were from stations in the west end of the Central Basin, I plotted the means for stations west of Erieau in addition to the cruise means for 1970 in Fig. 3. Apparently, the westerly stations may begin stratification at a slightly lower than average oxygen concentration, but the rate of decline is similar to the whole lake rate. In addition, I calculated oxygen depletion rates with data from only 2–3 stations near Erieau and compared these with rates calculated from cruise means. There were no consistent differences between the pairs of results, and the means of the two groups were not different (t test, $P > 0.01$). Apparently, the early depletion rates in 1929 and 1949–53 are comparable to those derived from cruise means of extensive but less frequent surveys after 1960.

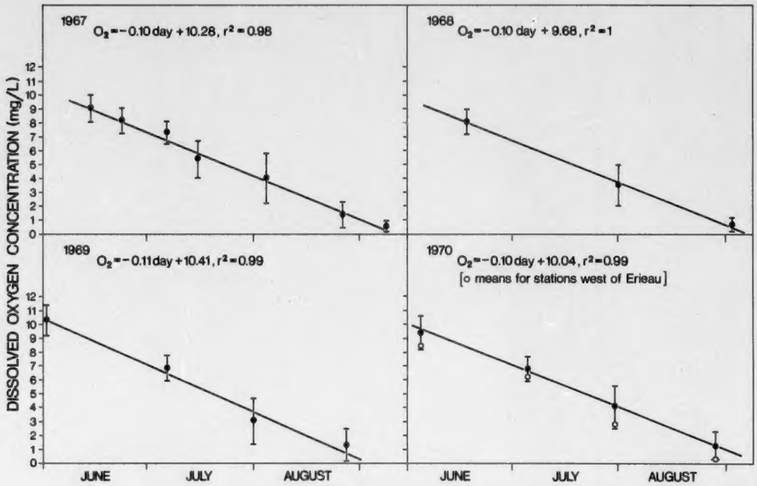

FIG. 3. Oxygen depletion in the hypolimnion of central Lake Erie 1967–70. Points and regression represent cruise means ±1 SD. Open circles in 1970 are for stations west of Erieau. Data for 1967, 1968, and 1969 are from C.C.I.W. reports (Canada Centre for Inland Waters, 1970a, b, c), and for 1970 from unpublished C.C.I.W. data.

There are moderate differences between the oxygen depletion rates published earlier (Dobson and Gilbertson 1971) and those calculated here. My depletion rates for 1960 and 1961 are higher than reported previously, while those for 1967, 1968, 1969, and 1970 are lower.

Additional Data

Data from CCIW cruises in 1972, 1973, 1975, 1977, and Center for Lake Erie Area Research cruises in 1974 and 1975 allowed additional depletion rates to be calculated:

Year	No. of cruises	No. of stations	Daily O_2 depletion rate
1972	3	16–22	0.10 mg/L
1973	2	24	0.07 mg/L
1974	4	32	0.11 mg/L
1975	5	25	0.08 mg/L
1977	5	38	0.10 mg/L

These results span the range of most of the available data as far back as 1949.

Historical Trends

A summary of the calculated rates of oxygen depletion is shown in Figure 4. The data have been converted to $\mathrm{mg/L \cdot mo^{-1}}$ in order to be comparable to other presentations. Figure 4 illustrates that the differences in oxygen depletion rates have been small. The slopes of regression lines for data of 1929–77, 1949–77, and 1949–70 are not significantly different from zero (t test, $P > 0.05$), but $0.03\ \mathrm{mg/L \cdot mo^{-1}}$ per year ($P < 0.01$) is obtained over the 1929–70 period because of the isolated position of the 1929 data. If the extreme years of 1962 and 1973 are taken as some measure of variability, any suggestion of a trend may be cavalier. This interpretation is in contrast to the analysis of Dobson and Gilbertson (1971) who concluded a clear historic trend resulted in the rate of oxygen depletion more than doubling from 1929 to 1970.

Effects of Climatic Variation

The degree of oxygen depletion which occurs in the hypolimnion of lakes is dependent on variables such as hypolimnion volume and the supply of organic matter or trophic state (Hutchinson 1938). The effect of hypolimnion volume or thickness is that the oxygen demand of sediments and falling seston is exerted on larger or smaller quantities of oxygen. Thus, the rate of change of oxygen concentration varies inversely with hypolimnion thickness. Also, as with any metabolic measurement, the rate of oxygen depletion is probably affected by temperature. In Lake Erie, changes in the rate of oxygen depletion have been assumed to indicate changes only in the general level of metabolism (trophic state). The purpose of this section is to examine the potential effects on the oxygen depletion rate of variations in climate, hypolimnion thickness, and hypolimnion temperature.

There were important climatic differences between

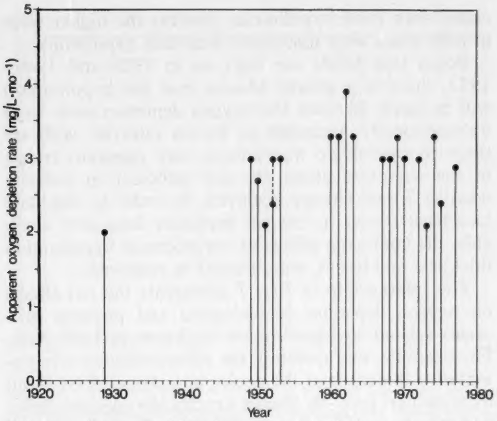

FIG. 4. Apparent historic oxygen depletion rates in the hypolimnion of central Lake Erie.

the years in which oxygen depletion rates were estimated in Lake Erie. One of the symptoms of these climatic differences, which may confuse analyses of a long-term trend, is the mean monthly outflow (Fig. 5). Mean monthly outflow for the period 1924–75 was 5.8×10^3 m^3/s with a range of ±20%. Because the flow or flushing rate of a lake helps determine the effect of phosphorus loading on chlorophyll concentration (Vollenweider 1976), there may be fluctuations in trophic state (e.g. chlorophyll) in the absence of any change in phosphorus loading. In years of low flow, the effects of phosphorus loading should be accentuated and vice-versa. The effects of flow variations may be damped in the other Great Lakes by their great volumes. Also, given the same relative change in phosphorus loading characteristics, the absolute change in chlorophyll, for example, is dependent on the original chlorophyll concentration. Thus, changes in trophic status may occur more rapidly and may be more noticeable in Lake Erie than in the other Great Lakes.

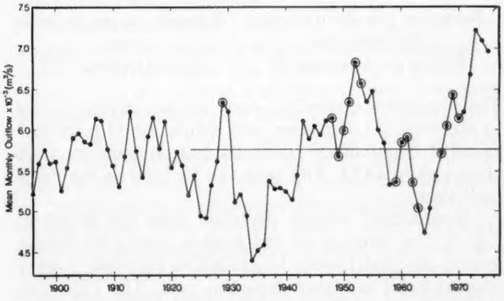

FIG. 5. Historic mean monthly outflow from Lake Erie. Circled points are years when oxygen concentration was measured in the hypolimnion. Horizontal line represents average flow after 1920. Data are from the Coordinating Committee on Great Lakes Basic Hydraulic and Hydrologic Data (1976).

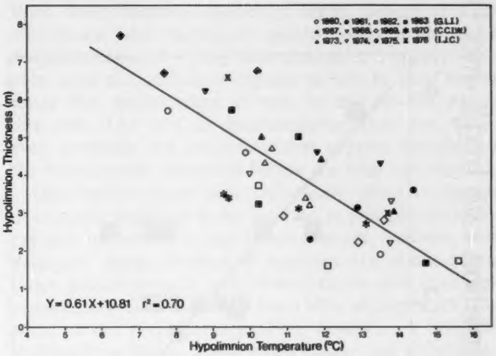

FIG. 6. Hypolimnion thickness and temperature in Central Lake Erie.

Figure 5 shows that there were long term oscillations which culminated in extreme high and low flows in 1929, 1952, 1973, and 1926, 1934, and 1964, respectively. These flow variations were associated with fluctuations in annual rainfall (Powers et al. 1960). Also, as might be expected, peak lake levels in June are highly correlated with outflow. During the years of historic oxygen depletion measurements, the range of lake levels was about 1 m; this may be important as the average hypolimnion thickness is only about 4 m. As shown in Fig. 5, the early depletion rates were measured in years with high flows, whereas the later rates tended to be in years with lower flows. The average flow for the years 1929 and 1948–53 was 6.3×10^3 m^3/s, but for 1959–63 and 1967–70, average flows were 5.5×10^3, and 6.1×10^3, respectively. Of the 7 early years, 6 had above average flow, but of the 9 later years, only 5 were above average. The main points are that important hydrologic conditions were not stable during the years in which oxygen depletion measurements were made and the early (low?) rates tended to be during high water periods, while the later (higher?) rates tended to be in low water periods. These factors may be insignificant to larger, deeper lakes, but may be important to Lake Erie.

Concurrent with differences in water level and flow, there were differences in both the thickness and temperature of Lake Erie's hypolimnion; these three factors exert synergistic effects on the oxygen depletion rate. Hypolimnion thickness (H_t) was estimated from bathythermographs or calculated from the combination of sounding depth, water sample temperature and depth at the top of the hypolimnion. Cruise mean (arithmetic) H_t and temperature for the summer months are shown in Fig. 6. The thickness of the hypolimnion ranged from 1.7 to 7.7 m with a grand mean of 4 m. Under the as-

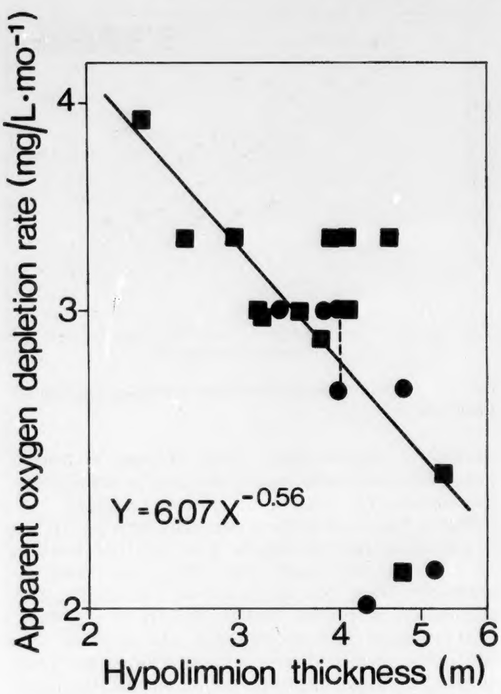

FIG. 7. Relationship between oxygen depletion rate and hypolimnion thickness in Central Lake Erie. Circles are for years in which thickness was estimated from temperature (1929–53). Dashed line connects depletion rates which developed in 1952.

sumption of a simple inverse proportionality, these thickness differences could alter the oxygen depletion rate. In addition, hypolimnion temperature varies considerably. The range of monthly mean temperatures was 6.5–15.6°C, while the range of seasonal mean temperature was 8.1–13.0°C. As in any other metabolic study, these temperature fluctuations should be accounted for. The inverse relationship between thickness and temperature means that for years in which the oxygen depletion rate is increased by a thin hypolimnion, the rate may be even greater due to a higher temperature. An additional result of Fig. 6 is that hypolimnion thickness can be estimated for years in which only bottom temperature was measured.

Figure 7 shows the inverse relationship between oxygen depletion rate and hypolimnion thickness in Lake Erie ($P < 0.01$). For the early years, 1929, 1949–53, in which only a few temperature measurements were available, the hypolimnion thickness was estimated from the relationship in Fig. 6. The lower oxygen depletion rates in the "early" years tended to be associated with thick hypolimnia, whereas the higher rates in later years were associated with thin hypolimnia.

When lake levels are high, as in 1929 and 1949–1953, there is a greater chance that the hypolimnion will be thick. Because the oxygen depletion rates were unintentionally measured at biased intervals with respect to hydrologic fluctuations, any apparent trends in the depletion alone are not sufficient to indicate whether a real change occurred. In order to elucidate long-term trends in oxygen depletion data now available, the confusing effects of variations in hypolimnion thickness and temperature should be removed.

The relationship in Fig. 7 represents the net effects on oxygen depletion of biological and physical processes related to hypolimnion thickness in Lake Erie. For example, extrapolating the relationship to a representative thickness of the cooler and deeper East Basin hypolimnion predicts almost exactly the oxygen depletion rate there (Charlton 1979). The effect of thickness in Fig. 7 is less than would be expected if all of the oxygen demand occurred at the sediments, but is consistent with approximately equal amounts of O_2 consumption in the water and at the sediments when the hypolimnion is 3–4 m thick. The fact that hypolimnion oxygen depletion in the Central Basin is fundamentally related to thickness means that the effects of thickness can be removed in order to clarify the effects of, for example, eutrophication.

Removing the effects of hypolimnion thickness on oxygen depletion would make the historical data relative to each other for the purpose of comparison, but the magnitude of residual differences between relative depletion rates can only be assessed in relation to an actual depletion rate. I apply the term "normalized" to depletion rates that are all relative to one single depletion rate and, thereby, made comparable to each other. Because oxygen depletion is proportional to thickness raised to −0.56, a "normalized" oxygen depletion rate can be calculated:

$$\frac{\text{Normalized (to 1970) oxygen depletion rate}}{(\text{1970 hypo thickness})^{-0.56}} = \frac{\text{Apparent oxygen depletion rate}}{(\text{hypo thickness})^{-0.56}}$$

The procedure normalizes each oxygen depletion rate to represent the depletion rate which would have prevailed if hypolimnion thickness and temperature were always as in 1970. Any year can be used as the "normal" year.

"Normalized" oxygen depletion rates are shown in Fig. 8. The removal of interference caused by fundamental physical factors has failed to elucidate a large upward trend to higher depletion rates. The 1929 rate may be too low (Carr 1962) and, standing alone, may give the appearance of a slight upward trend.

Some variability occurs in lakes with more consistent hypolimnia than Lake Erie (Thienemann 1928; Stewart 1976) and can be expected in Fig. 8. Thickness and temperature are only two of the important factors

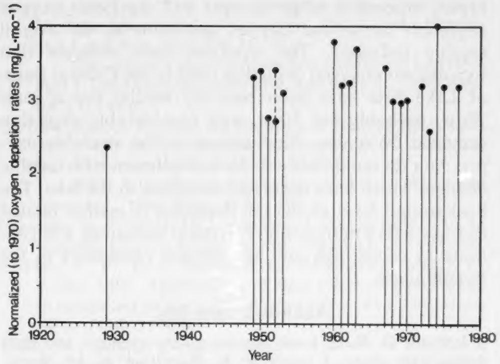

FIG. 8. Historic oxygen depletion rates in the hypolimnion of Central Lake Erie normalized to thickness conditions of 1970 (see text).

involved, others may be the relative importance of vertical oxygen transport to thick and thin hypolimnia, summer weather and resuspension of oxygen consuming sediments, incorporation of oxygen from East Basin incursions, mixing depth, and actual changes in trophic state. Nevertheless, hypolimnion thickness and temperature have a strong effect on hypolimnetic oxygen depletion in the Central Basin of Lake Erie. An apparent trend to higher depletion rates in the 1960s (Carr 1962) was caused by differences in water level, hypolimnion thickness, and temperature.

Discussion

The present calculations show that variation in the oxygen depletion rate in central Lake Erie may, in part, be explained by fluctuating physical factors. The hypothesis of a large long-term trend to increasing oxygen depletion does not seem to be supported by the present analysis of the available data.

To assess the lack of a trend, we need to know what oxygen depletion trend could have been expected, given trends in related data. The problem is the paucity of historic data for central Lake Erie on which to form a judgement. A review by Beeton (1965) showed that concentrations of sulfate and chloride have approximately doubled since 1930. An often cited paper by Davis (1964) seems to show a three-fold increase in the concentration of phytoplankton cells from the 1930s to the 1960s. These data are from a water treatment plant at Cleveland and represent water drawn from a depth of 13 m, 5.2 km offshore. Unfortunately, currents may cause these data to be more representative of West Basin conditions (Powers et al. 1960), and at times of low water there may have been a greater chance of sampling only from the epilimnion. In addition, the Cleveland area is known for elevated nutrient and plankton levels relative to the open lake.

Although there are many references to changes in West Basin benthos, species of algae, timing of algal abundance, and *Cladophora* growth, there is no actual documentation of a long-term change in a supply variable, such as particulate organic carbon in the Central Basin that would relate directly to the oxygen depletion rate. The lack of documentation does not, however, preclude the possibility that organic supplies to the hypolimnion increased before the lake was studied.

One factor which may potentially effect a change in oxygen conditions is the increase in phosphorus loading due to increased population, sewage facilities, and detergent usage. Present P loadings are about seven times greater than in precolonial times, and have approximately doubled since the 1930s (Chapra 1977). Most of the phosphorus loading, however, is into the shallow West Basin, where much uptake and sedimentation of phosphorus occurs (Burns 1976b). There is no basis for speculation on what fraction of the available P loaded to the West Basin actually becomes available in the Central Basin. The mechanism by which P loading may affect oxygen depletion is the stimulation of algal carbon fixation and maintenance of a higher average standing crop which may export more carbon to be oxidized in the hypolimnion. This fixed carbon is subject to losses by respiration, zooplankton grazing, and sedimentation. By incorporation into particles, some organic P and C is continually lost through sedimentation and burial, but the supply of C is essentially limitless, while the supply of P is limited by the loading rate and recycling characteristics. Because the annual rate of carbon fixation appears to be related to P loading in an asymptotic fashion (Vollenweider et al. 1974), changes in P loadings that are already high may have a relatively minor effect on the primary production of organic carbon, which may eventually contribute to the oxygen deficit. As expected from global correlations of oxygen deficits and P concentration (Rast and Lee 1978), changes in P loading should not result in exactly proportionate changes in oxygen depletion in the Central Basin. Dobson and Gilbertson (1971) suggested that the oxygen depletion rate increased by a factor only slightly more than two; the present analysis does not suggest an increase. Should there be expectations (of P loading effects) consistent with either analysis? The peculiarities of Lake Erie make a decision especially difficult because the linkages between P loading, organic material fluxes, and oxygen depletion have not been fully examined. For example, phytoplankton are most concentrated close to nutrient sources (inshore) in Lake Erie. The Central Basin hypolimnion receives organic matter from inshore and offshore areas, rivers, and the West Basin outflow. Storage of oxidizable material in sediments may cause oxygen depletion responses to lag behind changes in phosphorus loading. A description of how all these processes integrate to produce a depletion rate is as distant as a reliable prediction of hypolimnion response to changing epilimnion conditions. Clearly, modelling the oxygen depletion rate is a lengthy proposition.

Finally, a large change in Secchi depth might lead to expectations of change in the oxygen depletion rate (Lasenby 1975), but even this has not materialized in the Central Basin. Summer Secchi depths averaged 4.2 m in 1929, 7.3 m in 1948–53, 5.2 m in 1962, and 2.9 m in 1968. In 1969–71, summer Secchi depths averaged between 4–5 m (Dobson et al. 1974). Although the seasonal nature of this measurement makes comparison of years somewhat tenuous, there does not seem to have been a large long-term trend which would support expectations of changes in the oxygen depletion rate.

The oxygen depletion rates of lakes can be used as an index of trophic state. Hutchinson (1938, 1957) suggested upper limits that, for a 4 m hypolimnion in Lake Erie, are 1.25 mg/L·mo^{-1} for oligotrophy, and 2.50 mg/L·mo^{-1} for mesotrophy. The conclusion that the Central Basin of Lake Erie is eutrophic because the depletion rate is 3 mg/L·mo^{-1} would be misguided. The depletion rate limits are for small deep lakes with hypolimnion temperatures close to 4°C, whereas the average temperature for the Central Basin is 11.2°C; relative to Hutchinson's lakes, the Central Basin depletion rate is 1.66 times too high for comparative purposes. A depletion rate of 3 mg/L mo^{-1} at 11.2°C is equivalent to 1.8 mg/L·mo^{-1} at 4°C (assuming $Q_{10} = 2$) and falls within the limits of mesotrophy. Further, lakes such as Erie, with a thin hypolimnion and a low ratio of hypolimnion to epilimnion volume, tend to have relatively high volumetric oxygen depletion rates caused by their morphology alone (Hutchinson 1938; Thienemann 1928). Oxygen consumption occurs both in the water and at the sediments, and the hypolimnion thickness or volume helps determine the areal amount of consuming particles and initial oxygen supplies. Thus, the thickness of the hypolimnion is implicit in both the volumetric and areal expressions of oxygen depletion rates. A recent analysis of hypolimnion oxygen depletion in the Great Lakes and 19 small lakes indicated that hypolimnion thickness was slightly more important than trophic state (chlorophyll) in determining the amount and degree of oxygen depletion (Charlton, unpublished data). Clearly, hypolimnion oxygen indicates both trophic state and morphology; trophic scales based on oxygen alone are confusing.

Predictions of the exact response to nutrient loading changes in all areas of a large heterogenous lake are difficult. There is, however, little doubt that where water quality has been most degraded by excessive nutrients, control of nutrient loading will be beneficial (Vollenweider 1976). Models constructed under various assumptions about Lake Erie's oxygen response calculate that, while there may be some changes, significant oxygen depletion would still remain after annual P loadings are reduced by 9000 tons from current levels of 20 000 tons (Vallentyne and Thomas 1978). Previously, when P loadings increased by 6000–7000 tons (1950–70, Chapra 1977), no real change in oxygen depletion occurred.

There seems to be little reason at present to either expect immediate large changes in Lake Erie's oxygen depletion or to use oxygen depletion as an overall trophic indicator. The available data indicate that hypolimnion oxygen depletion rates in the Central Basin of Lake Erie have been basically similar for at least 20 yr, probably for 30 yr, and considerable depletion occurred 50 yr ago. Fluctuations in the available oxygen data do not indicate a clear correlation with trophic changes which have occurred elsewhere in the lake. The background level of oxygen depletion is mainly related to Lake Erie's morphology; physical variations will continue to cause high and low oxygen conditions in the hypolimnion.

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Genetic Changes in Hatchery Stocks of Brown Trout (*Salmo trutta*)

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RYMAN, N., AND G. STÅHL. 1980. Genetic changes in hatchery stocks of brown trout (*Salmo trutta*). Can. J. Fish. Aquat. Sci. 37: 82–87.

Preservation of the genetic characteristics of a population is one of the primary objectives of many fish stocking programs. Using starch gel electrophoresis we have tested for temporal gene frequency stability at two polymorphic loci coding for α-glycerophosphate dehydrogenase and creatine phosphokinase. Three Swedish hatchery stocks of brown trout (*Salmo trutta*) and field samples from natural populations corresponding to two of these stocks were analyzed. Highly significant allele frequency changes at both loci indicated considerable lack of intra-stock genetic homogeneity. In the light of these findings we emphasize the importance of using large numbers of actual as well as effective parents to avoid inadvertent genetic changes and inbreeding. No stock should be founded or perpetuated using less than approximately 30 parents of the least numerous sex in any generation.

Key words: inbreeding, genetic drift, gene bank, electrophoresis, stocking, trout

RYMAN, N., AND G. STÅHL. 1980. Genetic changes in hatchery stocks of brown trout (*Salmo trutta*). Can. J. Fish. Aquat. Sci. 37: 82–87.

Un des principaux objectifs de plusieurs programmes de stockage de poissons est la préservation des caractéristiques génétiques de la population. Utilisant l'électrophorèse sur gel d'amidon, l'auteur a vérifié la stabilité temporelle de fréquence des gènes à deux loci polymorphiques pour α-glycérophosphate déshydrogénase et créatine phosphokinase. Trois stocks de pisciculture suédoise de truites brunes (*Salmo trutta*) et des échantillons prélevés sur le terrain à même des populations naturelles correspondant à deux de ces stocks ont été examinés. Des changements hautement significatifs de fréquence des allèles aux deux loci indiquent un manque sérieux d'homogénéité génétique intrastock. Devant ces constatations, nous faisons ressortir l'importance d'utiliser un grand nombre de parents, tant réels qu'efficaces, afin d'éviter des changements génétiques accidentels et la consanguinité. On ne devrait pas fonder ou perpétuer de stock avec moins de 30 parents environ du sexe le moins nombreux dans toute génération.

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ARTIFICIAL propagation followed by massive release of hatchery reared fish is frequently practiced in the management of many fish species, notably the salmonids. The destruction of spawning sites caused by hydroelectrical power plant construction has necessitated the development of hatchery programs aimed at minimizing ecological and economical damage caused by drastic numerical reductions or complete eradication of fish populations. In light of the global energy crisis and the need for efficient use of aquatic and marine protein resources, more extensive hatchery release programs than practiced today can be foreseen (Moav et al. 1978).

A hatchery stock is frequently the only existing remnant of a population whose ecological basis for survival has been damaged (e.g. by damming, drying out, or blocking migration to spawning streams). In these cases a hatchery functions as a gene bank, conserving and multiplying often unique biological resources. It is of fundamental importance for the breeding program to prevent inadvertent damage of the gene pool through loss of genetically determined population characteristics.

There is an obvious risk of creating genetic changes as a result of the switch from natural reproduction to artificial propagation. First, selection pressures are drastically altered when the fish breed, hatch, and spend part of their life in the highly protected hatchery environment. Second, the reproductive capacity of many fishes, potentially producing large numbers of offspring from few parents, brings about the possibility of genetic deterioration as a result of inbreeding. These problems have been recognized and discussed by several authors (see e.g. Rasmuson 1968; Ryman 1970; Kincaid 1976; Allendorf and Utter 1979). However, there has been no serious attempt that we are aware of to estimate either the extent of genetic changes actually going on in hatchery stocks, or whether or not the genetic composition of hatchery stocks are really typical for the natural populations they are assumed to represent. Allendorf and Utter (1979) found a remarkably low level of electrophoretically detectable genetic variation in a hatchery population of rainbow trout (*Salmo*

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TABLE 1. Sampling information.

Origin and name of stock/population	Stocking	Sample	Year of hatching	Sample particulars
Lake Arevattnet	Stock founded by stripping wild spawners in late 1960s. Offspring from those spawners were parents to the present hatchery samples hatched in 1976 and 1977.	Field sample	1967–72	Collected 1976 with gill nets of varying mesh sizes. Sample cannot contain planted fish.
		Hatchery stock	1976	Both year classes were derived from essentially the same set of parents
		Hatchery stock	1977	
Lake Kallsjön	Continuous propagation and release in Lake Kallsjön. Breeders recruited by trapping "wild" spawners and by raising hatchery fish in artificial ponds.	Hatchery stock	1972	These two year classes are likely to be from different sets of parents but detailed records on parentage were not routinely kept.
		Hatchery stock	1974	
River Storboströmmen	Continuous propagation and release in River Storboströmmen. Breeding procedures similar to those practiced for the Lake Kallsjön stock.	Hatchery stock	1972	These two year classes are likely to be from different sets of parents.
		Hatchery stock	1974	
		Field sample	1976	Collected 1978 by electro-shocking. May contain recaptured hatchery fish.

gairdneri) which had been subjected to reduced population size for a long period of time and an ongoing program of intense directional selection for several characters. The low amount of genetic variability in this stock was coupled with poor survival during the early life of the zygote. Although it is likely that the hatchery procedures practiced for that stock resulted in a drastic loss of genetic variation, this hypothesis cannot be verified because of the lack of data on the genetic variability in the original population.

In our ongoing study of the genetic structure of brown trout (*Salmo trutta*) we have accumulated genetic data on various natural populations and some hatchery stocks. The purpose of the present study was to test for genetic heterogeneities in hatchery stocks. We present here gene frequency comparisons between repeated samples from three different stocks and samples from natural populations corresponding to two of these stocks. The results indicate that unwanted drastic genetic changes have been induced by the stocking procedures.

Materials and Methods

Our samples represent various derivatives of populations from three localities in central–northern Sweden, viz. Lake Arevattnet, Lake Kallsjön, and River Storboströmmen (Fig. 1 and Table 1). River Storboströmmen is a tributary to River Indalsälven, and Lake Kallsjön is one of the upper lakes in the River Indalsälven drainage system; Lake Arevattnet belongs to the upper part of the River Umeälven drainage system. Both of the major river systems drain into the Baltic Sea.

Construction of hydroelectric power plants has destroyed the access to a considerable fraction of the brown trout (*Salmo trutta*) spawning sites in the River Indalsälven drainage. To compensate for the loss of natural reproduction, hatchery fish are released every year. Two separate stocks named "Kallsjön" and "Storboströmmen" have been extensively propagated and used for planting in the Lake Kallsjön and the River Storboströmmen, respectively.

Lake Arevattnet has been famous for its large-sized brown trout. When average size and population number seemed to decline, the local fishery authorities initiated a stocking program with the two-fold intention of establishing a program to preserve the genetic characteristics of this population (i.e. a gene bank) and producing fish for release in Lake Arevattnet. In 1977 the local fishery officer initiated the genetic analysis of the "Arevattnet" hatchery stock upon receiving a batch of fry for release and finding that they had both an unusually high mortality and "looked different" from typical Lake Arevattnet brown trout. Fortunately, meaningful allele frequency comparisons could be made since field samples from Lake Arevattnet had previously been electrophoretically analyzed within the scope of our ongoing study of genetic variability in natural populations of brown trout.

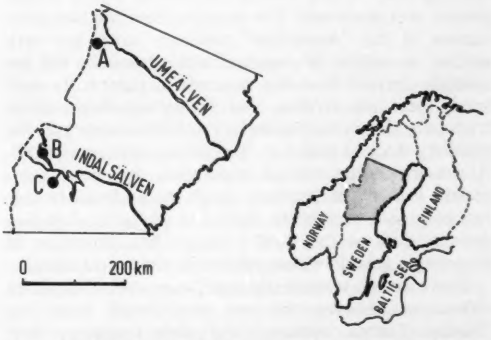

FIG. 1. The River Indalsälven and River Umeälven drainage systems. A: Lake Arevattnet, B: Lake Kallsjön, and C: River Storboströmmen. Location of area indicated on map of Scandinavia.

TABLE 2. Allele frequency variation within "strains." The P values are from conventional 2 × 2 chi-square contingency comparisons (Yates' correction. df = 1) computed from allele and phenotype counts at the *AGP-2* and *CPK-1* loci, respectively.

Location and type of sample		Year of hatching	Number of fish	Locus and allele frequency					
				AGP-2			*CPK-1*		
				100	*50*		*100*	*115*	
Lake Arevattnet	Field sample (1976)	1967–72	86	0.89	0.11	$P<0.001$	0.17	0.83	$P<0.001$
” ”	Hatchery stock	1976	86	1.0	0	$P = 1$	0.57	0.43	$P>0.05$
” ”	” ”	1977	103	1.0	0		0.55	0.45	
Lake Kallsjön	” ”	1972	20	0.98	0.02	$P>0.05$	0.61	0.39	$P>0.05$
” ”	” ”	1974	62	1.0	0		0.39	0.61	
River Storboströmmen	” ”	1972	25	0.96	0.04	$P>0.05$	0.55	0.45	$P<0.001$
” ”	” ”	1974	61	1.0	0	$P = 1$	0.08	0.92	$P<0.001$
” ”	Field sample (1978)	1976	12	1.0	0		1.0	0	

For the purpose of the present report the variation at two polymorphic loci which could be used for allele frequency comparisons between subsamples from the same stock or population are given. These loci, predominantly expressed in muscle tissue, are *AGP-2* coding for α-glycerophosphate dehydrogenase with two alleles designated *100* and *50*, and *CPK-1* coding for creatine phosphokinase, also with two alleles which are designated *100* and *115* (Allendorf et al. 1976, 1977). Tissue samples from fish of various year-classes of the hatchery stocks were obtained from the appropriate rearing stations. Tissue extracts were prepared and horizontal starch gel electrophoresis was accomplished following the methods of Utter et al. (1974). Buffer systems, gel preparation, and staining procedures are given in Allendorf et al. (1977). Allele frequencies at the *AGP-2* locus were estimated by direct "allele counting," while the allele frequencies at *CPK-1* was estimated from the square root of the frequency of *115/115* homozygotes (Allendorf et al. 1977). Specimens collected in the field were aged through otolith annulae counts.

Results

The data of Table 2 indicate considerable genetic heterogeneity within sets of collections where homogeneity was presumed. The samples from the two year-classes of the "Arevattnet" hatchery stock are very similar, as would be expected with groups of fish essentially derived from the same set of parents. In contrast, there are striking and highly significant allele frequency differences between the field sample and the hatchery stock at both loci. The polymorphism at *AGP-2*, present in the natural population, has been completely lost in the hatchery stock. In addition to this loss of genetic variability, there is a dramatic allele frequency shift at the *CPK-1* locus. The intention of founding a gene bank has obviously not been fulfilled.

There are no statistically significant allele frequency differences between the two year-classes from the "Kallsjön" stock. Although the allele frequency shift at the *CPK-1* locus appears conspicuous this difference might well be attributed to chance effects explainable by the small sample sizes.

Comparing the two year-classes from the "Storboströmmen" hatchery stock there are drastic and highly significant allele frequency differences at the *CPK-1* locus. The 1974 year-class also differs remarkably from the field sample but there is no statistically significant difference between the field sample and the 1972 year-class (chi-square test, $P > 0.05$). This latter lack of significance should be evaluated with some caution considering the very small sample sizes involved in that comparison. However, neither the limited sample sizes or the circumstance that the origin of the fish in the field sample is unknown invalidate the conclusion of pronounced genetic heterogeneity among different derivatives of the River Storboströmmen stock.

The distribution of sample sizes coupled with the low level of variability at the *AGP-2* locus in the "Storboströmmen" stock complicates the statistical evaluation of the differences at this locus. When the 1972 and 1974 groups are compared using Fisher's exact test for independence (Sokal and Rohlf 1969, ch. 16), the exact (one-tailed) probability $P = 0.083$ for the observed distribution. When testing the 1972 group versus the pooled results from the 1974 group and the field sample (i.e. the samples fixed for the *AGP-2* (*100*) allele), the corresponding probability is $P = 0.064$. Thus, though the observed differences at the *AGP-2* locus are not strictly significant they might indicate that preexisting variability at this locus has been lost from the "Storboströmmen" stock in the course of a short period of time.

Discussion

When discussing the preservation of genetic variation, it should be stressed that the primary objective is not just the variability at a few electrophoretically detectable loci but at all polymorphic loci. Electrophoretic loci are used only as easily scorable markers that potentially reflect the status of a larger fraction of the whole genome.

The present study has demonstrated considerable genetic heterogeneity among samples previously assumed to be representing identical gene pools. In two out of the three cases which were available for testing, we have detected drastic allele frequency changes within a hatchery stock as well as differences between a hatchery stock and the natural population it was assumed to typify. These differences were displayed despite the fact that some of our sample sizes are very small and the statistical power for detection of true differences is consequently poor. In our opinion these findings are alarming and compel careful consideration of present practices as well as further studies aimed at identifying the factors responsible for the changes. Temporal allele frequency shifts have not been observed in any of the natural populations from which we have multiple samples (Ryman et al. 1979, and unpublished data).

At present it is not possible to determine whether the observed allele frequency changes were caused by genetic drift, selection, or both. However, on the basis of our general knowledge of brown trout hatchery breeding procedures we feel that the present findings might well be explained by genetic drift and founder effects induced by the use of too few parents in the founding and perpetuation of the stocks. The high mortality and "uncharacteristic morphology," i.e. typical inbreeding effects, which were observed in the "Arevattnet" stock support this conclusion. Inbreeding depression affecting viability has been reported in many fishes including such species as Atlantic salmon (*Salmo salar*) (Ryman 1970) and rainbow trout (Aulstad and Kittelsen 1971; Kincaid 1976) which are closely related to the brown trout.

The present findings, which indicate that hatchery stocks may rapidly lose the genetic variability they were intended to preserve, urge a serious discussion about methods for accomplishing the various goals associated with the gene bank concept. How many parents should then be used to avoid inbreeding? Although various aspects of this problem has been discussed by many authors, e.g. Nei et al. (1975) from a general evolutionary point of view and by Allendorf and Utter (1979) and Kincaid (1976) from the perspective of fish breeding, we feel that a few comments are needed in the light of the present findings. Theoretically, an infinite number of parents should be used but this is impractical. A more realistic approach to the problem is to determine when only little more genetic variability is gained by using additional parents. This matter is usually discussed in terms of *effective* population size defined as the size of an "ideal" population having the same amount of drift and inbreeding as that occurring in the population actually considered.

The effective number of parents (N_e) is influenced by several factors (see e.g. Crow and Kimura 1970), the sex ratio among the breeders being the most conspicuous one in the context of fish breeding. As shown by Wright (1931)

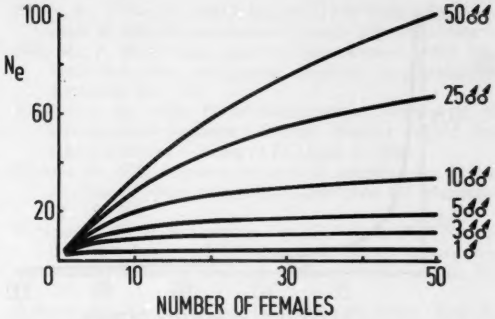

FIG. 2. Effective number of parents (N_e) as a function of the actual numbers of female and male (selected values) parents breeding.

$$N_e = \frac{4\, N_{♂}\, N_{♀}}{N_{♂} + N_{♀}}$$

where $N_{♂}$ and $N_{♀}$ are the actual numbers of male and female parents, respectively. With a limited number of breeders the largest effective number of parents is obtained when both sexes are equally frequent. When sex ratios are highly skewed the effective number of parents is best approximated by the least numerous sex (Fig. 2). Even if a large number of females were bred with a single male, the effective number of parents would only be four.

Considering a specific allele at a single locus, the expected allele frequency change from one generation to another is proportional to the inverse of twice the effective number of parents $(1/(2N_e))$. Therefore, from the genetic point of view maximizing N_e, or rather minimizing $1/(2N_e)$, should be one of the primary objectives of a sound hatchery stock breeding program. Also, the increase in inbreeding per generation (ΔF) is determined by

$$\Delta F = \frac{1}{2N_e},$$

and the relation between ΔF and N_e is given in Fig. 3. There is a practical limit at which ΔF is only slightly affected by a further increase of N_e and this limit occurs approximately at 40 to 60 effective parents.

From the perspective of hatchery fry production only, the number of females is often regarded as the most limiting factor. In general, least effort is consequently invested in keeping a sufficiently large number of males. We recommend that no stock should be founded or perpetuated using less than 30 males and 30 females chosen at random from the stock in any generation. These figures must be regarded as minimum numbers. When dealing with extremely valuable stocks, e.g. a single hatchery stock representing the last remnant of a natural population, considerably higher numbers of both sexes are urged.

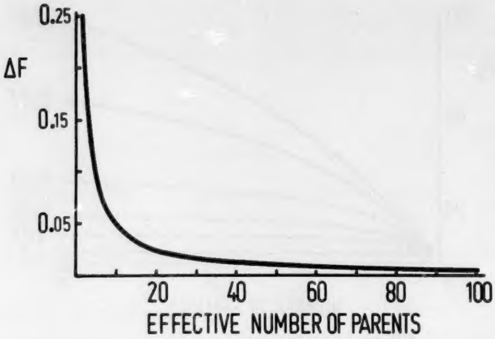

FIG. 3. Increase of inbreeding per generation (ΔF) as a function of the number of effective parents.

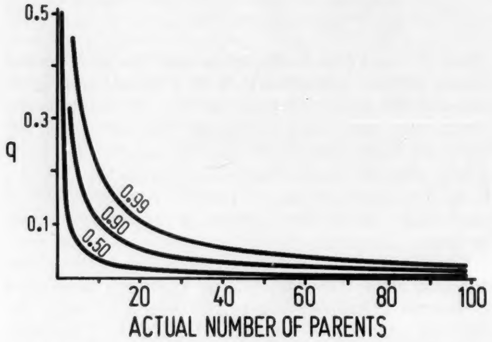

FIG. 4. The relationship between the actual number of parents sampled at random from a panmictic population, the frequency of the least common allele (q) at a two-allele locus, and the probability (0.50, 0.90, and 0.99) that both alleles at this locus occur among the parents.

Our discussion about effective number of parents should not give the misleading impression that the *actual* number of parents (N_a) is unimportant. While the magnitude of inbreeding and allele frequency change is completely determined by N_e, the probability that a specific allele will not be lost is determined by N_a. Any stocking program includes the transplantation of genotypes into new environments, and at present there is no way to predict which specific alleles will be beneficial in the new environment. In some cases it might be more important that an allele is just present in a population than that it occurs in a frequency close to the original one (cf. Nei et al. 1975). Natural selection has a chance to adjust the frequency of an allele that is present, while this is impossible if the allele was lost during stocking.

Considering a single locus with two alleles occurring at the frequencies p and q ($p + q = 1$) the approximate probability not to have both alleles present in a sample of n individuals from a panmictic population is $p^{2n} + q^{2n}$, and the probability that they are both present is one minus this quantity. Only few fish are required to give a high probability that both alleles are included in the sample when allele frequencies are intermediate, while large numbers of parents are needed when p or q is small (Fig. 4). In practice, the actual number of polymorphic loci, the number of alleles, and the allele frequencies are unknown. Consequently every additional parent used contributes to the conservation of genetic variability. The amount of "classical inbreeding," as measured by average heterozygosity, may remain essentially unchanged at the same time as the number of alleles is drastically reduced. Using the assumptions of the so-called infinite allele model, Nei et al. (1975) estimated that the genetic variability contained in a random sample of 100 parents was reduced by approximately 50% as measured by the average number of alleles/locus but only by 0.5% ($1/(2N_e)$) as measured by average heterozygosity.

We have emphasized the importance of using large numbers of parents (actual as well as effective) for the maintenance of the genetic characteristics of a population or stock. However, large numbers of parents alone are not sufficient for a successful stocking program. As pointed out by several authors, a detailed understanding of population structure within the species is a basic prerequisite for the formulation of effective management programs (Behnke 1972; Manlove et al. 1976; Smith et al. 1976; Ryman et al. 1977, 1979; Allendorf and Utter 1979). In rivers or lakes inhabited by more than one genetically distinct population of a species "hatcheries may inadvertently break down the reproductive barriers between these stocks, established by thousands of years of natural selection, by forced mixing or favoring one or a few stocks over the others" (Behnke 1972). Reproductively isolated populations coexisting in a very small lake provides a good example of such a situation for the brown trout (Allendorf et al. 1976; Ryman et al. 1979).

Our results stress the need for awareness of the genetic problems involved in fishery management activities. Gene bank or stocking program should normally be started after a detailed analysis of the genetic structure of the populations involved. Continued surveillance of the genetic composition of hatchery stocks should be maintained. Electrophoresis provides an excellent tool for this type of analyses, and we foresee an extensive use of such techniques in the planning and carrying out of sound fishery management programs.

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Role of Gut Flora in the Transfer of Amino Acids Through a Marine Food Chain

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FONG, W., AND K. H. MANN. 1980. Role of gut flora in the transfer of amino acids through a marine food chain. Can. J. Fish. Aquat. Sci. 37: 88–96.

The gut of the sea urchin *Strongylocentrotus droebachiensis* has between 2×10^8 and 6×10^9 bacteria/mL of gut contents. When these bacteria are present, radioactive carbon fed to the urchins as either glucose or cellulose appears in all of the protein amino acids of the gonads. However, when the gut flora is suppressed by a mixture of antibiotics, injection of the sea urchins with radioactive glucose results in the labeling of some of the amino acids (nonessential amino acids) but not others (essential amino acids). These results imply that: (a) sea urchins have the ability to digest cellulose, probably with the aid of the gut flora; (b) intestinal microorganisms can synthesize essential amino acids; and (c) amino acids of microbial origin are available to the sea urchins. The amino acid compositions of (i) kelp (*Laminaria longicruris*), (ii) sea urchin intestinal microflora, and (iii) sea urchins, were determined over a yearly cycle. The amino acid composition of kelp and microbes were compared as a source of nutrient for the sea urchins, using as indications: overall similarity in compositions, essential amino acid index, and percentage of total amino acid that is essential. All three comparative methods show that the microbial protein is of higher nutritive value than the kelp protein.

Key words: amino acids, nitrogen, bacteria, kelp, *Laminaria longicruris*, sea urchin, *Strongylocentrotus droebachiensis*

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L'intestin de l'oursin commun *Strogylocentrotus droebrachiensis* contient entre 2×10^8 et 6×10^9 bactéries par mL de contenu intestinal. Quand ces bactéries sont présentes, le carbone radioactif que l'on donne aux oursins, soit sous forme de glucose ou de cellulose, apparaît dans tous les acides aminés protéiques des gonades. Cependant, quand on supprime la flore intestinale au moyen d'un mélange d'antibiotiques, l'injection de glucose radioactif dans des oursins marque certains acides aminés (acides aminés non essentiels) mais non d'autres (acides aminés essentiels). Ces résultats donnent à croire que: (a) l'oursin commun peut digérer la cellulose, probablement à l'aide de sa flore intestinale; (b) les micro-organismes intestinaux ont le pouvoir de synthétiser les acides aminés essentiels; et (c) l'oursin commun a à sa disposition des acides aminés d'origine microbienne. Nous avons déterminé, durant un cyle annuel, la composition en acides aminés (i) du varech (*Laminaria longicruris*), (ii) de la microflore intestinale de l'oursin commun et (iii) des oursins eux-mêmes. Nous avons comparé la teneur en acides aminés du varech avec celle des microbes comme source de nourriture pour l'oursin commun, utilisant les indicateurs suivants : similitude générale de composition, indice d'acides aminés essentiels et pourcentage d'acides aminés totaux qui sont essentiels. Ces trois méthodes s'accordent à démontrer que les protéines microbiennes ont une valeur nutritive supérieure à celle des protéines du varech.

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THE importance of microbes in detritus food chains is well recognized (Fenchel 1972; Mann 1972). Many vertebrate herbivores, especially the ruminants, have a gut microflora that assists in the digestion and absorption of their food (Hungate 1966). However, the role of microbes in the digestive processes of invertebrates is less well understood. Many insects have symbiotic microorganisms in their guts (House 1974) and it has been shown that the microbes synthesize nutrients which the host insects can use (Henry 1962). Similar studies on the role of intestinal microbes in the nutrition of marine animals are rare.

In Eastern Canada, sea urchins (*Strongylocentrotus droebachiensis*) are found feeding primarily on marine macrophytes. Indeed it has been suggested that sea urchin grazing determines the composition and distribution of seaweed and seagrass communities in many parts of the world (see Breen and Mann 1976). However, many of the marine macrophytes on which sea urchins live are low in protein content (Burkholder

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1956; Burkholder et al. 1971; Chapman and Craigie 1977), and sea urchins in their natural environments are likely to experience nitrogen limitations (Mann 1979). Physiological adaptations have been claimed to occur in sea urchins, that would make possible the selective assimilation of nitrogen (Propp 1975; Lilly 1975).

Weese (1926) first reported the presence of large numbers of bacteria in the gut of the green sea urchin, *Strongylocentrotus droebachiensis*. His observation was confirmed by those of many scientists (see Lawrence 1975) including our own observations on local populations of the species. Although many investigators have since studied the role of urchin intestinal microflora in carbohydrate digestion, none have published on the possible role played by microbes in nitrogen transfer along the kelp to sea urchin food chain.

The purpose of this study was to establish the role played by the intestinal microflora on the amino acid metabolism of sea urchins. Radiotracers were employed to examine the essential amino acid requirements of the sea urchins, and the utilization of gut microflora as a source of essential amino acids. Seasonal distributions in the amino acid composition of kelp, gut flora of urchins and of sea urchins were also monitored to compare the nutritive values of kelp and microbes as a source of amino acids for the urchins.

Materials and Methods

All samples of kelp (*Laminaria longicruris*) and sea urchins (*Strongylocentrotus droebachiensis*) were collected at Fox Point, St. Margaret's Bay, N.S.

Essential Amino Acid Requirements of the Sea Urchin

The sea urchins, provided with an excess of kelp, were acclimatized for 1 wk in running seawater at ambient sea temperature. Experiments were carried out on two groups of sea urchins collected in April.

The first group of five sea urchins was transferred to membrane-filtered (0.45 μm) seawater at 8°C to which 50 mg penicillin G and 40 mg streptomycinsulfate/L had been added. As a check on this procedure, the gut contents of two urchins which has been treated in this way for 2 d were examined and found to have less than 1×10^3 bacteria/mL, while untreated animals were found to have 2.5×10^8 bacteria/mL. After 2 d, 1.85×10^6 Bq of U-^{14}C-glucose (specific activity 1.21×10^{10} Bq/mmol) was injected into the coelom of each of the urchins through the peristomial membrane. The sea urchins were then incubated for 3 d in the dark in air-tight bottles each containing 900 mL of antibiotic seawater aerated with filtered and CO_2-free air. The CO_2 leaving the bottles was collected in 0.5 N KOH.

The second group of two urchins was treated in the same manner as the first, except that each of the animals was injected with 1.85×10^5 Bq of U-^{14}C-phenylalanine (specific activity 1.898×10^{10} Bq/mmol) instead of labelled glucose and incubated for 24 hr only.

The protein fractions of whole bodies of sea urchins were isolated and purified by the method of Shibko et al. (1967).

Intestinal Microflora of Urchins as a Source of Amino Acids

The urchins used in this study were collected in late September 1976, provided with excess amounts of kelp and acclimatized for a week in running seawater at ambient temperature before testing.

They were then transferred into containers (2 L) supplied with running seawater at 8–12°C, and with a turnover time approximately once every 5 min to prevent the accumulation of labeled compounds. Observable particulate matter in the containers was removed by frequent siphoning. After a day, two urchins (urchins #1 and 2) were each fed with 1.85×10^6 Bq of finely powdered U-^{14}C-cellulose (specific activity 1.665×10^5 Bq/mg, ICN Pharmaceuticals), and a third (urchin #3) with 1.85×10^6 Bq of U-^{14}C-glucose (specific activity 1.21×10^{10} Bq/mmol, Amersham Corp.). The radioactive cellulose and glucose were embedded in 5% Bacto-agar (Difco Lab.) which had been dissolved in the supernatant fluid of an homogenate from kelp and hot water (1:1). Small discs of approximately 0.5 cm in diameter and 1–2 mm in thickness were formed, and were passed gently onto the tube feet of the urchins and forceps. During subsequent days, the animals were given small pieces of kelp (about 0.2 g/d) in the same manner. Uningested pieces were removed after an hour. Urchins #1, 2, and 3 were incubated for 8, 14, and 3 d, respectively. The unusually long incubating periods were to allow sufficient time for food digestion, microbial assimilation, and utilization of materials of microbial origin. The animals were kept in the dark with minimum disturbance. Feeding and cleaning procedures were carried out under red light.

At the end of incubation, the gonads of urchins were collected and the protein fractions isolated (Shibko et al. 1967). To avoid contamination from microbes in the gut of the urchins, only the protein fractions from the gonads of urchins were used in the study.

Sample Preparation for Amino Acid Analysis

Each month the blades of three plants of *Laminaria longicruris* were washed free of attached fauna, freeze-dried, and ground to a fine powder. The samples were stored in vials at −18°C until ready for analysis.

The method used to collect bacteria from the gut of the urchins was adapted from studies of rumen bacteria (Weller 1957; Purser and Buechler 1966; Hoogenraad and Hird 1970). The following procedures were carried out on urchins within 3 h after collection. Gut contents, solid and fluid, of 20–30 large sea urchins were collected in a cylinder kept in ice. This was diluted with known amount of ice-cold (0–4°C) membrane filtered seawater (0.45 μm). The suspension, after transferring into conical flasks, was shaken vigorously with glass beads (3 mm diameter) on a Burrell Wrist Action Shaker for 20 min to release bacteria from particles and separate filamentous microbes into individual units. Samples were then taken to count the numbers of bacteria in a Petroff-Hausser counting chamber with a phase microscope. The suspension was filtered through a coarse fiberglass net (0.25 mm^2) to remove coarse residues which were washed with more filtered seawater. The filtrate and washings were centrifuged in a Servall refrigerated centrifuge (0°C) at $163 \times g$ for 10 min to bring down the protozoa and plant material. The residue was washed twice with more filtered seawater. The combined supernatant was then filtered through Whatman No. 1 filter paper and again through a millipore filter of pore size 10 μm. The filtrate was then centrifuged at 16300 × g for 25 min to sediment "bacteria." The bacterial paste was transferred into a small test tube and freeze-dried.

In all of the separation procedures emphasis was placed on obtaining a relatively pure bacterial fraction at the expense of quantitative yields and complete representation of samples. However, microscopic examinations showed that some amount of contamination, presumably kelp fragments, were still visible and accounted for about 30–40% of the visible particles.

Four urchins collected fresh each month were killed and the perivisceral fluid collected. The gut contents were washed off under a slow running tap. The perivisceral fluid with the entire urchin (including shell) were freeze-dried and ground into a fine powder with a mortar and pestle.

AMINO ACID ANALYSIS

Samples were hydrolyzed with constant boiling HCl in evacuated sealed tubes for 24 h at 110°C. Mercaptoacetic acid was added to each sample to prevent the oxidation of tryptophan (Matsubara and Sasaki 1969). Nor-leucine was added as an internal standard. The hydrolysates were evaporated to dryness *in vacuo* over solid NaOH at room temperature. Amino acid analyses were carred out on an amino acid analyzer according to the methods of Spackman et al. (1958), after the samples had been passed through hot-water washed millipore filters (0.45 μm). Cysteine was not analyzed.

Preliminary experiments indicated that the large quantities of mineral salts, mainly $CaCO_3$ and $MgCO_3$, in urchins do not cause significant reduction in the quantitative recoveries of amino acids although the shapes of the acidic amino acid peaks were distorted. The presence of D-mannitol, but not other compounds, in the kelp may cause serious reduction in the recovery of certain amino acids (Fong and O'Dor 1979). Correction factors have been calculated and applied to the results of amino acid analyses of kelp (see Fong 1978). Due to the limited size of samples, tests for compounds that might interfere with amino acid analysis in the bacterial samples were not performed.

SEPARATION AND RADIOASSAY OF LABELED AMINO ACIDS

Isolation of amino acids, in the proteins of urchins injected or fed radioactive substrates, was carried out on the preparative column of the amino acid analyzer described by Fong (1978). To radioassay separated amino acids, 1 mL of the fractions containing acidic or neutral amino acids, or 0.5 mL of basic amino acids with 0.5 mL of water were mixed with 10 mL Phase Combining System (Amersham/Searle Corp.), and counted with a Nuclear Chicago ISOCAP 300 liquid scintillation counter. Radioactivities of the background were monitored and results were corrected for background counts.

Results and Discussion

ESSENTIAL AMINO ACID REQUIREMENTS OF THE SEA URCHIN

Concentrations and specific activities of amino acids isolated from the protein hydrolysates of four urchins treated to inhibit gut flora are shown in Table 1. The results are expressed as DPM/μmol C, to allow direct comparison of the relative rate of amino acid biosynthesis. Radioactivity was detected in alanine, aspartic acid, glutamic acid, serine, glycine, proline, and cysteine of the 17 amino acids determined. 6.2% of the injected radioactive carbon was incorporated into amino acids. In the two urchins injected with U-^{14}C-phenylalanine, radioactivity was found only in the tyrosine and phenylalanine fractions.

We may therefore conclude that threonine, valine, methionine, isoleucine, leucine, tyrosine, phenylalanine, tryptophan, lysine, histidine, and arginine are essential to the diet of sea urchins, since they cannot be synthesized from glucose. In this respect, sea urchins resemble most other animals.

Although arginine cannot be synthesized from glucose (Table 1), the sea urchin might be able to synthesize it if the proper precursors were provided. High concentrations of urea have been reported in the perivisceral fluids of many species of urchins (Fechter 1973). Chen and Baltzer (1958) detected the presence of ornithine in the embryos of sea urchins. Thus, it is likely that a functional urea cycle exists in urchins. Citrulline and ornithine are present in many species of seaweeds (Reuter 1961; Young and Smith 1958), so the biosynthesis of arginine from these intermediate compounds of the urea cycle may well occur. However, it is not known whether arginine synthesized in this way would be available to the urchin for protein synthesis.

URCHIN GUT FLORA AS A SOURCE OF ESSENTIAL AMINO ACIDS

All amino acids, essential and nonessential, isolated from the gonadal protein of urchins with normal gut floras showed radioactivities above background when the animals were fed radioactive substrates. The only exception (Table 2) was an arginine fraction with no detectable label. The nonessential amino acids tended to exhibit higher specific activities than the essential ones: four times greater for urchins fed labeled cellulose and two times greater for those fed labeled glucose. However, for the essential amino acids to become labeled several events would have to take place: (a) digestion of the U-^{14}C-cellulose by means of cellulase, (b) synthesis of essential amino acids by organisms other than the urchins themselves, and (c) utilization of the synthesized amino acids by the urchins. The origin of the cellulase is not known for certain. Lewis (1964) found no cellulase in extracts of the gut of *Diadema antillarum*, and Prim and Lawrence (1975) concluded that mixed bacteria isolated from the gut of *Lytechnis variegatus* could not digest cellulose. It is not known whether other species of sea urchins can digest cellulose, but Foulds and Mann (1978) showed that the mysid shrimp *Mysis stenolepis* can do so, probably with the aid of gut flora.

TABLE 1. Concentrations and specific activities of amino acids obtained from the protein fractions of urchins (treated to inhibit gut flora) after the injection of 1.85×10^6 Bq of U-^{14}C-glucose or 1.85×10^6 Bq of U-^{14}C-phenylalanine.

	Injected with U-^{14}C-glucose						Injected with U-^{14}C-phenylalanine			
	Average concentration (μmol/100 mg protein)		Specific activity (DPM/μmol C)				Concentration (μmol/100 mg protein)		Specific activity (DPM/μmol C)	
Amino acid	*x*	SD	Urchin #1 (13.6 g)	Urchin #2 (10.8 g)	Urchin #3 (7.5 g)	Urchin #4 (6.2 g)	*x*	SD	Urchin #6 (23.4 g)	Urchin #7 (44.7 g)
ASP	53.0	11.0	1717	1922	4524	4530	50.8	5.7	0	0
THR	36.6	3.7	0	0	0	0	37.5	2.6	0	0
SER	35.0	2.7	580	602	922	2024	33.3	4.7	0	0
GLU	92.7	15.4	1272	1074	3370	3722	74.3	0.7	0	0
PRO	45.8	9.2	0	86	212	288	26.0	2.6	0	0
GLY	65.9	11.2	428	320	1094	868	42.5	1.5	0	0
ALA	48.3	2.2	3462	3930	13750	19046	42.4	0.4	0	0
VAL	30.4	2.2	0	0	0	0	33.6	0.5	0	0
MET	3.2	0.5	0	0	0	0	3.3	0.8	0	0
CYS	N.D.[a]		+[b]	+	+	?[c]	N.D.		0	0
ILE	22.7	2.2	0	0	0	0	28.7	1.8	0	0
LEU	41.0	5.5	0	0	0	0	45.3	2.0	0	0
TYR	16.9	1.4	0	0	0	0	19.5	0.1	527	754
PHE	22.5	6.3	0	0	0	0	27.1	0.1	3852	3771
TRP	1.2	0.3	0	0	0	0	1.3	0.0	0	0
LYS	38.4	7.2	0	0	0	0	40.9	8.5	0	0
HIS	10.1	1.7	0	0	0	0	12.0	2.1	0	0
ARG	42.5	4.4	0	0	0	0	35.6	5.2	0	0

[a]Not quantified; [b]+ indicates incorporation of label, but not quantified; [c]? indicates uncertainty.

TABLE 2. Combined concentration and individual specific activities of amino acids isolated from the gonadal protein of sea urchins fed with U-^{14}C-cellulose or U-^{14}C-glucose.

	Average gonad concentrations (μmol/100 mg protein)		Urchin fed U-^{14}C-cellulose		Urchin fed U-^{14}C-glucose	
Amino acid	Mean (*n* = 3)	SD	Urchin #1 (11.9 g)	Urchin #2 (15.9 g)	Urchin #3 (20.3 g)	Amino acid requirements (from Table 1)
ASP	46.0	5.7	930	1430	410	Nonessential
THR	35.9	2.3	170	210	110	Essential
SER	29.8	3.2	500	560	160	Nonessential
GLU	81.0	7.4	380	870	190	Nonessential
PRO	26.2	4.4	280	210	100	Nonessential
GLY	50.9	1.0	470	430	90	Nonessential
ALA	48.2	11.2	760	920	410	Nonessential
VAL	34.7	2.4	130	230	140	Essential
MET	9.4	6.0	290	320	150	Essential
CYS	N.D.[a]	N.D.[a]	+[b]	+	+	Nonessential
ISL	33.7	1.6	190	120	140	Essential
LEU	52.0	3.0	130	110	120	Essential
TYR	21.8	1.9	50	60	110	Nonessential
PHE	29.5	3.1	30	110	90	Essential
TRP	2.9	1.2	30	90	100	Essential
LYS	33.6	11.0	60	90	130	Essential
HIS	11.8	1.3	50	10	10	Essential
ARG	36.2	2.6	40	0	20	Essential

[a]N.D. indicates not quantified; [b]+ indicates radioactivity above background.

The organisms responsible for synthesis of essential amino acids are most likely to be bacteria. Ciliates are also present in the gut, but these have essential amino acid requirements similar to those of higher animals. Bamford and James (1972) and West and Jeal (1973) showed that in the gut of urchins D-alanine is actively absorbed against the concentration gradient, and this is taken as evidence that D-alanine is naturally available (Lawrence 1975). Since D-alanine is a characteristic component of the cell walls of bacteria (Strominger et al. 1967) but not of plant or animal protein (Corrigan 1970) this strongly suggests that the urchins take up microbial protein.

AMINO ACID COMPOSITION OF KELP, BACTERIA, AND SEA URCHINS

Results of monthly analyses of 16 naturally occurring amino acids in kelp, bacteria, and sea urchins are shown in Fig. 1. In kelp, glutamic acid, aspartic acid, and alanine were the most abundant amino acids, while histidine and methionine usually occurred in low concentrations. There were obvious seasonal fluctuations in composition, with alanine and proline falling from 20 and 10% by weight in midwinter to 8 and 5% in midsummer. The pattern follows that of the seasonal variations in organic nitrogen in kelp (Chapman and Craigie 1977). Most other amino acids showed the reverse trend and were more abundant in summer.

In bacteria (Fig. 2), the numbers ranged from $2 \times 10^8 \cdot mL^{-1}$ to $6 \times 10^9 \cdot mL^{-1}$, which is of the same order of magnitude as rumen samples (Hungate 1966) but lower than the figures given by Lasker and Giese (1954) for *Strongylocentrotus purpuratus* ($2.6 \times 10^{11} \cdot mL^{-1}$). The bulk amino acid composition of bacteria samples changed little throughout the year. Total microbial protein was 23–38% of sample dry weight, and when compared with analyses of pure cultures of bacteria (Stewart et al. 1963) suggests that the bacterial samples are only 40–60% pure. However, the contaminant is mainly kelp which has a relatively low protein content, and it is estimated that less than 10% of the protein in the samples was from kelp. The relative constancy of microbial alanine suggests that contamination is not a problem.

In sea urchins, glutamic acid, glycine, and arginine are the most common amino acids. There are seasonal changes in composition, though these are smaller than in kelp. The most marked changes occur at the time of spring reproduction (Fig. 3) and is 3–4 mo out of phase with changes in the kelp.

KELP VS. BACTERIA AS PROTEIN SOURCE FOR SEA URCHINS

Biological efficiency of protein synthesis may be indexed by the ratio of nitrogen assimilated to nitrogen supplied. This may be estimated for each essential amino

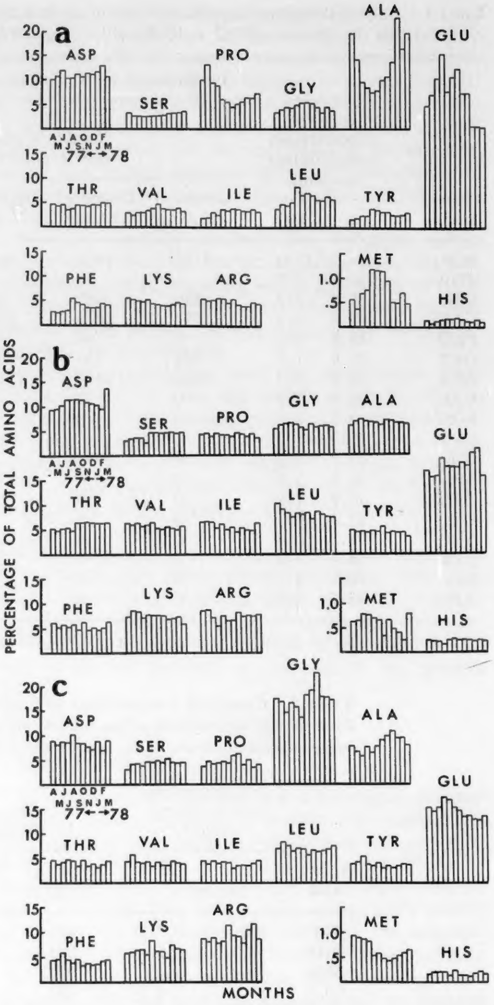

FIG. 1. Monthly analysis of the amino acid composition of (a) *Laminaria longicruris*, values are means of three plants; (b) bacteria isolated from the guts of sea urchins (*Strongylocentrotus droebachiensis*); and (c) *S. droebachiensis* (whole animals), values are means of four animals. All samples were collected at Fox Point, N.S., and results are expressed as percentage by weight of total amino acids.

acid by the expression (Mitchell and Block 1946)

$$I = \frac{P_1 - P_2}{P_2} \times 100$$

where P_1 is the percentage of an amino acid in kelp

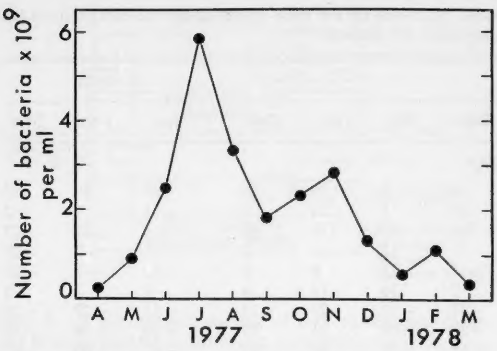

FIG. 2. Seasonal variation in the number of bacteria per unit volume of the gut content of sea urchins, estimated by direct count method.

or bacteria, and P_2 is the percentage of that amino acid in an urchin. The essential amino acid showing the lowest negative index value is considered to the limiting amino acid. The overall index of efficiency will be low when one or more essential amino acids are scarce in the food.

An alternative approach is to consider the energy cost of protein synthesis from dietary proteins. This will be least when the composition of dietary proteins and body proteins are most similar. Similarity of two amino acid spectra may be calculated from the goodness-of-fit formula:

$$\chi^2 = \sum_{i=1}^{n} \frac{(O_i - E_i)^2}{E_i}$$

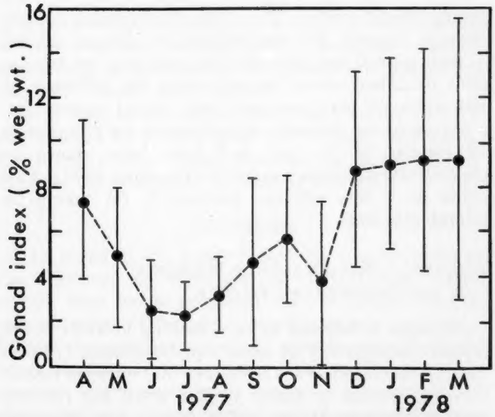

FIG. 3. Monthly variation of gonad index (ratio of gonad net weight to total wet weight × 100) of *Strongylocentrotus droebachiensis* at Fox Point, N.S. Points are means ± SD.

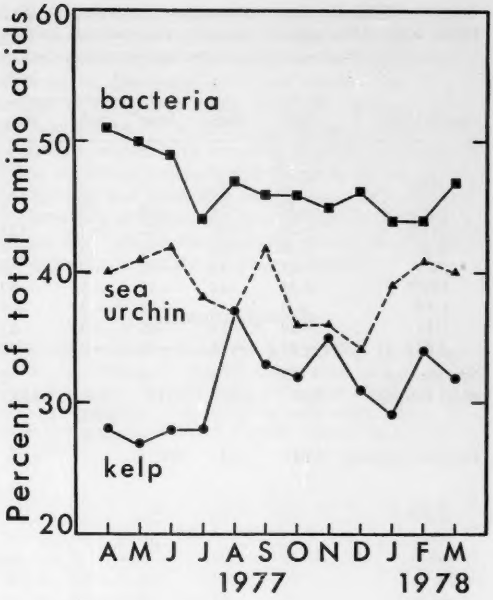

FIG. 4. Essential amino acids as a percentage of the total amino acids by weight in kelp (*L. longicruris*), bacteria, and sea urchins (*S. droebachiensis*).

where O_1 is the percentage by weight of an amino acid in either kelp or bacteria, and E_i is the corresponding value in a sea urchin. A low chi-square value indicates a high degree of resemblance in composition, and vice-versa. Tables 3 and 4 show that the microbial protein is a better amino acid source for the urchins than is the kelp protein, and the result is not affected by seasonal variations in amino acid compositions. Figure 4 shows that bacteria have a high proportion of essential amino acids than kelp at all times of the year. The conclusion that the essential amino acid profiles of bacteria, unlike those of sea grasses (Burkholder 1956) or seaweeds (Burkholder et al. 1971) are complete enough to meet the needs of animals that can and do feed on bacteria is not new (Purser 1970). However, it should be noted that no allowance has been made for variations in the efficiency of absorption of different amino acids.

It has been argued that sea urchins are not true herbivores, and will take amino acids from animal food whenever they can get it. However, a study of nitrogenase activity in the guts of freshly collected urchins (Guerinot et al. 1977; Guerinot 1979) showed that almost all the urchins showed some nitrogenase activity. Since this activity would be suppressed by the presence of considerable amounts of nitrogen compounds in the gut (Taha 1964) it is clear that very few urchins were

TABLE 3. Essential amino acid indices of (a) kelp, and (b) bacteria; calculated on the basis of percentage deviations from the amino acids of the urchins. Negative values indicate limiting amino acids for urchins.

	1977									1978		
Amino acid	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
					(a) Kelp							
THR	0	13	5	−21	−13	36	−4	30	20	57	39	12
VAL	−31	−57	−28	−23	−17	23	1	34	8	11	1	−2
MET	−39	−61	−22	−11	123	105	62	176	98	−6	17	−27
ILE	−58	−50	−34	−35	−9	−17	12	6	2	−11	−2	−27
LEV	−43	−43	−40	−22	20	−4	12	8	4	−14	−7	−21
PHE	−36	−44	−52	−35	49	2	30	14	4	−4	7	−3
LYS	−3	−11	−19	−21	−3	−47	−33	−29	−15	−43	−27	−29
HIS	−29	−55	−45	−35	23	−30	107	21	27	−39	−38	−39
ARG	−39	−38	−42	−29	−32	−59	−49	−42	−45	−63	−60	−47
No. limiting	8	8	8	9	5	5	3	2	2	7	5	8
Most limiting	ILE	MET	PHE	ILE PHE HIS	ARG	ARG	ARG	ARG	ARG	ARG	ARG	ARG
2nd most limiting	LEU	VAL	HIS	—	VAL	LYS	LYS	LYS	LYS	LYS	HIS	HIS
					(b) Bacteria							
THR	17	30	23	17	7	96	44	102	63	111	72	40
VAL	49	7	51	50	47	105	28	42	63	57	25	54
MET	−33	27	−9	6	34	16	−30	63	4	−23	−61	20
ILE	47	73	50	63	42	23	82	22	44	38	26	36
LEU	50	11	15	18	17	15	49	9	37	23	15	2
PHE	43	15	0	19	53	7	97	30	49	30	25	47
LYS	24	47	33	12	45	−7	31	27	46	−3	9	6
HIS	47	10	5	−20	85	17	64	86	127	22	14	22
ARG	−5	7	−21	−30	−10	−42	−30	−11	−9	−29	−40	−10
No. limiting	2	0	2	2	1	2	2	1	1	3	2	1
Most limiting	MET	—	ARG	ARG	ARG	ARG	ARG MET	ARG	ARG	ARG	MET	ARG
2nd most limiting	ARG	—	MET	HIS	—	LYS	—	—	—	MET	ARG	—

TABLE 4. Comparison of the similarities of the amino acid compositions of kelp and gut flora of urchin with that sea urchin by the goodness-of-fit test.

	χ^2 Value from goodness-of-fit test	
Month	Kelp and urchin	Bacteria and urchin
1977		
Apr.	51.0	14.3
May	52.6	11.3
June	39.3	9.1
July	36.5	10.8
Aug.	18.7	11.8
Sept.	30.4	15.3
Oct.	35.4	23.7
Nov.	31.2	18.5
Dec.	35.0	24.3
1978		
Jan.	44.3	20.6
Feb.	32.5	20.2
Mar.	36.8	14.1

getting animal protein. The work on nitrogenase activity strongly suggests that the urchins are nitrogen limited in their growth and reproduction, and that the adaptations described above for increasing the efficiency of utilization of plant nitrogen may be of utmost importance to the animals. Amoebocytes are plentiful in all regions of the gut and have been shown to phagocytose particulate material (Gardiner 1972). This could be a very effective mechanism for taking up microbial protein.

ECOLOGICAL SIGNIFICANCE OF MICROBES IN THE TRANSFER OF NITROGEN

Nitrogen is believed to be a limiting nutrient in the primary productivity of many aquatic systems (Morris 1974; Hutchinson 1975). The idea that nitrogen limitation may extend to higher trophic levels has recently been proposed by Mann (1979). Hence, any ecological process that contributes to more efficient utilization of nitrogen in food chains is highly significant. A mixture

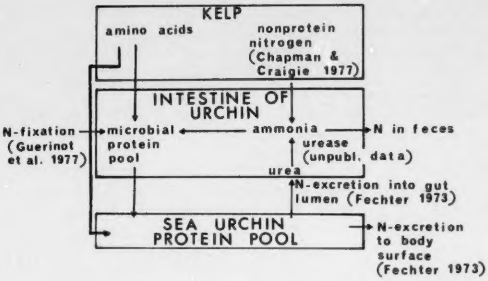
KELP
amino acids
nonprotein nitrogen (Chapman & Craigie 1977)
INTESTINE OF URCHIN
N-fixation (Guerinot et al. 1977)
microbial protein pool
ammonia
N in feces
urease (unpubl. data)
urea
N-excretion into gut lumen (Fechter 1973)
SEA URCHIN PROTEIN POOL
N-excretion to body surface (Fechter 1973)

FIG. 5. A hypothetical cycling of flow of nitrogen along the kelp → microbe → sea urchin food chain.

of food amino acids that is close to the mixture found in the tissues of an animal will be used more efficiently by that animal than will a mixture that is deficient in one or more components. The evidence given above suggests that a herbivore with an active gut microflora is likely to be ecologically more efficient than one without. The presence of a microflora in the gut of urchins helps to explain the ability of urchins to live on a diverse intake of plant tissue (see Lawrence 1975). The microbes can be viewed as an important transformer serving to create a more stable nutrient source for the urchins (Burkholder 1971).

Another possible role for the microbes is in increasing the total amount of amino nitrogen. It is now known (Guerinot et al. 1977; Guerinot 1979) that the gut flora of *Strongylocentrotus droebachiensis* carries out N_2 fixation and that labeled nitrogen subsequently appears in the gonads of the urchins. There are also high concentrations of nitrate in *Laminaria*, especially during winter, and it is quite possible that the gut flora can use such inorganic dissolved compounds (Fig. 5). It appears logical for some of the excess carbohydrate in kelp to be used in maintaining microbes, which in return help to increase both the quality and quantity of nitrogen available to the urchins.

Such mechanisms are a good illustration of the view put forward by Reichle et al. (1975) that "ecosystems function to expend readily available energy to minimize the constraints imposed by limiting nutrients."

Conclusions

The thesis of this paper is strongly supported by all the evidence, but there are one or two areas where further work would be needed for a wholly conclusive demonstration of the role of bacteria in this food chain. Ideally, the transfer of the ^{14}C label to bacteria would be demonstrated by measuring radioactivity of gut organisms, and monitoring its decline as lebeled bacteria are assimilated. To show that certain essential amino acids that are in short supply do actually limit the growth of the urchins, it would be necessary to conduct rigorous and lengthy feeding experiments.

Bearing in mind these reservations, it seems exceedingly probable that the bacterial flora of the gut of sea urchins greatly assists the urchins in making the maximum use of *Laminaria* as a food source. The protein content of *Laminaria* varies seasonally and is at times very low indeed. By synthesizing essential amino acids, by making available in bacterial protein a mixture of amino acids that is close to that found in the sea urchin, by digesting and extracting energy from cellulose, and by converting inorganic nitrogen to organic compounds, the gut flora greatly increases the ecological efficiency and competitive success of these echinoids.

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Simulations of Energy Flow Through the Amictic Female Rotifer *Brachionus rubens* Ehrbg.

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A model is developed (i) to integrate a set of experimental observations concerning the energy flow through the amictic female rotifer *Brachionus rubens* Ehrbg.; (ii) to identify inconsistencies in the data; (iii) to understand better the energy dynamics of this organism and the impact of the environment on it; and (iv) to determine the direction of further experimental and theoretical studies. Simulations of energy flow through this organism are generated for various concentrations of food (the alga *Chlorella vulgaris*), constant during its life span. It is shown that the experimental data for the immature female are self-consistent but that the experimental instantaneous values of total production for the mature female are undervalued. Consequently, Pilarska's instantaneous values of food assimilation and the instantaneous coefficients of energy conversion efficiency are undervalued for the mature female. Using sensitivity analysis we find that the model is highly sensitive to changes in (listed in order of importance) (i) the instantaneous value of food consumption, (ii) the instantaneous coefficient of food assimilation efficiency, (iii) the life span, and (iv) the egg calorific value. The model is relatively insensitive to changes in (i) the initial body calorific value, (ii) the age at maturity, (iii) the time interval between two successive acts of reproduction, and (iv) the instantaneous value of respiration. Specific parameters are identified as needing remeasurement.

Key words: model, simulation, bioenergetics, growth, reproduction, rotifer, *Brachionus rubens*, sensitivity

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Le modèle présenté ici a été élaboré dans le but (i) d'intégrer une série d'observations expérimentales sur le flux énergétique à travers le rotifère femelle amictique *Brachionus rubens* Ehrbg.; (ii) d'identifier les contradictions dans les données; (iii) de mieux comprendre la dynamique énergétique de cet organisme et la façon dont il est affecté par l'environnement; et (iv) d'orienter les études expérimentales et théoriques futures. On crée des simulations de flux énergétique à travers cet organisme pour diverses concentrations de nourriture (l'algue *Chlorella vulgaris*), qu'on maintient à un niveau uniforme durant toute sa vie. Nous démontrons que les données expérimentales touchant la femelle immature sont en accord entre elles, mais que les valeurs instantanées expérimentales de production totale chez la femelle mature sont sous-estimées. Il en résulte que chez la femelle mature, les valeurs instantanées de Pilarska d'assimilation de nourriture et les coefficients instantanés d'efficacité de conversion d'énergie sont également sous-estimés. A l'analyse de sensibilité, nous constatons que le modèle est très sensible à des changements des facteurs suivants (donnés par ordre d'importance) : (i) valeur instantanée de consommation de nourriture, (ii) coefficient instantané d'efficacité d'assimilation de nourriture, (iii) durée de vie et (iv) valeur calorifique des oeufs. Le modèle est relativement insensible à des changements des facteurs suivants : (i) valeur calorifique corporelle initiale, (ii) âge de maturité, (iii) intervalle de temps entre deux actes reproducteurs successifs et (iv) valeur instantanée de respiration. Nous mentionnons des paramètres spécifiques ayant besoin d'être mesurés de nouveau.

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FULL understanding of the complex process of energy and matter flow through ecological communities requires knowledge of the bioenergetics of particular species inhabiting these communities. The filter-feeding rotifer *Brachionus rubens* Ehrbg. is found in great numbers in eutrophic bodies of water such as fish ponds, settling ponds, and sewage treatment plants. It plays an important role in the ecological productivity of these systems as a consumer and as a food basis for subsequent trophic levels (Pilarska 1971, 1972). The aim of this paper is to develop a mathematical model of energy flow through the amictic female *B. rubens* throughout most of its life span excluding a brief nonreproductive period preceding death. The model is based on experimental data obtained by Pilarska (1971, 1977a, b, c, and unpublished data). It is assumed, following from Pilarska's experimental conditions, that the female rotifer feeds on the alga *Chlorella vulgaris* and that all parameters describing the rotifer's environment are constant during its life span. Different, but constant, food concentrations are considered since feeding conditions strongly influence the organism's potentials for growth and reproduction.

The model is developed (i) to integrate Pilarska's experimental data on the energy flow through this organism; (ii) to identify inconsistencies in these data; (iii) to understand better the energy dynamics and filtration strategy of the organism and the impact of the environment on these processes; and (iv) to determine the direction of further experimental and theoretical studies. Considering the lack of bioenergetic models for rotifers, a group of organisms ecologically significant as suspension feeders (cf. Jörgensen 1966; Hilbricht-Ilkowska 1977), the development of this model seems to be desirable from the general ecological point of view. Such a model can also be used in developing simulations of energy flow through complex aquatic ecosystems.

Formulation of the Model

GENERAL STRUCTURE

The model is constructed as follows:

$$\frac{dC_c}{d\tau} = C(W, \phi)$$

$$\frac{dA_c}{d\tau} = U(\tau, \phi)\,\frac{dC_c}{d\tau}$$

$$\frac{dR_c}{d\tau} = R(W, \phi)$$

$$\frac{dP_c}{d\tau} = \frac{dA_c}{d\tau} - \frac{dR_c}{d\tau}$$

$$W(\tau, \phi) = W_0(\phi) + P_c(\tau, \phi) - n(\tau, \phi)\cdot W_0(\phi) \tag{1}$$

where

τ [days] — age of the female

ϕ [(cell/mL) × 10^6] — food concentration

W [mcal] — calorific value of the female body including eggs

C_c, A_c, R_c, P_c [mcal][2] — values of food consumption, food assimilation, respiration and total production, respectively, cumulated over the age interval $[0, \tau]$

C, R [mcal] — instantaneous values of food consumption and respiration

U — instantaneous coefficient of food assimiliation efficiency

n — number of eggs laid to age τ

W_0 [mcal] — egg calorific value

The notation used in the equations is consistent with that recommended within the IBP (Grodzinski et al. 1975). The above structure follows from the general model of energy flow through an animal organism (Majkowski 1978; Klekowski et al. 1980).

EXPERIMENTAL MEASUREMENTS

The experimental data utilized during model development are presented in Table 1. The experimental techniques involved and their reliability are discussed in full detail by Pilarska (1971, 1977a, b, c); therefore, we include in this paper only a brief description.

Laboratory cultures of *B. rubens* were cultivated at a temperature of 20°C ± 0.4°C in suspensions of the alga *C. vulgaris* (concentrations as indicated in Table 1).

The body calorific value of the amictic female was calculated by multiplying dry body weight by the calorific equivalent of one unit of dry body weight. In a similar way the egg calorific value was determined. The calorific equivalent of one unit of dry body weight, assumed by Pilarska to be independent of actual body weight, age, and food concentration, was found by combustion in a microbomb calorimeter of 10 000 preovigerous amictic female rotifers obtained from a culture fed on *C. vulgaris* (concentration of 1 million cells/mL). The calorific equivalent of one unit of egg dry weight, assumed by Pilarska to be independent of food concentration and type of egg, was found by combustion in the same calorimeter of 20 000 dormant eggs obtained from the same culture.

To determine the dry body weight we selected either 50 or 100 amictic females of each age indicated in Table 1 from each culture (characterized by different food concentrations). After being washed in distilled water, they were desiccated over CaO at 55°C and then weighed. The weight of the diploidal egg, which is often attached to the body of the amictic female, was determined from the difference between the dry weights of females carrying eggs and females without eggs. Direct weighing of diploidal eggs was impossible due to the difficulty of collecting enough unattached eggs. To verify the results, we also calculated weights indirectly as a product of the volume and the specific weight. The results from direct weighing and indirect calculations were very similar.

Instantaneous values of food consumption were measured by isolating single rotifers for 2 h in suspensions at the same food concentrations as their original cultures. The number of algae in the experimental and control vessels before and after the rotifers were introduced was determined by counting the cells in a Thom chamber. Repro-

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[2] 1 cal = 4.1868 J.

TABLE 1. The experimental data on energy flow through the amictic female rotifer *B. rubens* (at various constant food concentrations, ϕ) obtained by Pilarska (1971, 1977a, b, c, and unpublished data).

ϕ [(cell/mL) × 10^6]	Time [h]	Age [h]	W^d [mcal]	C^e [mcal/d]	R^e [mcal/d]	P^e [mcal/d]
0.012		diploidal egg	0.23			
	$\tau_m = 68.9^a$	$0 \leq \tau \leq 12$	0.28	0.40	0.15	0.06
	$\tau_L = 88.1^b$	$12 < \tau \leq 24$	0.30	0.43	0.18	0.06
	$\tau_e = \infty^c$	$24 < \tau \leq \tau_m$	0.47	0.47	0.21	0.06
		$\tau_m < \tau \leq \tau_L$	0.59	0.48	0.26	0.07
0.03		"	0.24			
	$\tau_m = 53.9$		0.31	0.60	0.15	0.13
	$\tau_L = 79.3$		0.38	0.62	0.18	0.13
	$\tau_e = \infty$		0.55	0.66	0.21	0.14
			0.61	0.70	0.26	0.14
0.06		"	0.24			
	$\tau_m = 50.1$		0.36	0.74	0.15	0.17
	$\tau_L = 93.6$		0.45	0.78	0.18	0.18
	$\tau_e = 36.0$		0.64	0.82	0.21	0.17
			0.70	0.82	0.26	0.16
0.10		"	0.25			
	$\tau_m = 47.9$		0.36	0.81	0.15	0.21
	$\tau_L = 120.4$		0.47	0.91	0.18	0.20
	$\tau_e = 36.0$		0.64	0.87	0.21	0.17
			0.72	1.00	0.26	0.21
0.40		"	0.32			
	$\tau_m = 41.8$		0.45	1.37	0.14	0.26
	$\tau_L = 189.4$		0.58	1.41	0.16	0.24
	$\tau_e = 16.8$		0.74	1.50	0.20	0.23
			0.85	1.71	0.25	0.24
0.60		"	0.33			
	$\tau_m = 35.1$		0.46	1.36	0.14	0.28
	$\tau_L = 178.3$		0.60	1.58	0.16	0.27
	$\tau_e = 14.4$		0.67	1.63	0.20	0.24
			0.86	1.71	0.26	0.28
1.00		"	0.33			
	$\tau_m = 31.6$		0.47	1.70	0.14	0.28
	$\tau_L = 195.7$		0.60	1.79	0.16	0.28
	$\tau_e = 12.0$		0.68	1.89	0.20	0.25
			0.85	1.94	0.26	0.35

[a] Age at maturity.

[b] Life span excluding a brief nonreproductive period preceding death.

[c] Time interval between two successive acts of reproduction.

[d] Measured at the end of the period for the first three age intervals and in the middle of the period for the fourth age interval.

[e] The mean value for each age interval.

duction of alga in the course of the experiment was taken into account in the calculations. To express the food consumption in energy units, we determined the calorific value of an average cell of *C. vulgaris* utilizing the method of combustion in a microbomb calorimeter.

Instantaneous values of respiration were calculated on the basis of oxygen consumption measured for single female rotifers and the oxycalorific coefficient (Ivlev 1945). Oxygen consumption was measured in stoppered Cartesian divers.

Instantaneous values of total production were calculated for the immature female on the basis of increases in body calorific value and for the mature female by counting the number of eggs laid within a given time interval by a given number of females. Since some eggs remain attached to the females, correct estimation of the number of eggs laid was difficult. Utilizing the egg calorific value determined previously, the instantaneous value of total production was calculated. Such a method for estimating total production was justified by the fact that body growth other than reproductive growth was not observed in the mature female.

Average values for age at maturity, time interval between two successive acts of reproduction and life span excluding a brief nonreproductive period were determined

TABLE 2. The values of parameters c_I and c_{II} (for various constant food concentrations, ϕ) obtained by fitting function (2) to the experimental data (Table 1).

ϕ	0.012	0.030	0.060	0.100	0.400	0.600	1.000
c_I	0.54 ± 0.04	0.77 ± 0.01	0.87 ± 0.02	1.10 ± 0.04	1.75 ± 0.07	1.82 ± 0.07	2.01 ± 0.03
c_{II}	0.20 ± 0.07	0.20 ± 0.01	0.13 ± 0.03	0.24 ± 0.04	0.29 ± 0.07	0.28 ± 0.07	0.18 ± 0.03
SS^a	0.74×10^{-3}	0.03×10^{-3}	0.37×10^{-3}	1.13×10^{-3}	7.13×10^{-3}	7.26×10^{-3}	1.46×10^{-3}

[a] SS — Sum of squares of residuals.

TABLE 3. The experimental instantaneous coefficients of food assimilation efficiency, U, of the female rotifer for various constant food concentrations, ϕ, and age intervals, τ.

ϕ	0.012	0.030	0.060	0.100	0.400	0.600	1.000
$0\text{ h} \leq \tau \leq 12\text{ h}$	0.53	0.47	0.43	0.44	0.29	0.31	0.25
$12\text{ h} < \tau \leq 24\text{ h}$	0.56	0.50	0.46	0.42	0.28	0.27	0.25
$24\text{ h} < \tau \leq \tau_m$	0.57	0.53	0.46	0.39	0.29	0.27	0.24
$\tau_m < \tau \leq \tau_L$	0.69	0.57	0.51	0.47	0.29	0.32	0.31

by observation of numerous individual amictic female rotifers.

DETERMINATION OF PARAMETERS

Food consumption — Several authors (cf. Sushchenya 1975) point out that under constant environmental conditions the instantaneous value of food consumption of a filter-feeder may be assumed to be an increasing power function of its body calorific value:

$$(2) \quad C = c_I W^{c_{II}}.$$

There is some question as to whether or not the body calorific value should include the value of a developing egg if present. Experimental observations indicate that the female rotifer increases its food consumption during egg development (Pilarska 1971), therefore we assume that W includes the calorific value of an egg, if present.

Pilarska's experimental data are approximated well by the power function (2); the values of parameters c_I and c_{II}, obtained from fitting the function to the data, as well as the sums of squares of residuals, are presented in Table 2. Many authors assume that parameter c_{II} is independent of food concentration (cf. Sushchenya 1975). This is verified by our calculations, which show the parameter c_{II} to vary only very slightly from its mean value of 0.22 ± 0.02 (see Table 2). Considering the insensitivity of the model to changes in this parameter (see Sensitivity Analysis section), the above mean value is taken to be applicable for all food concentrations and the values of parameter c_I are calculated once again (Fig. 1, symbol '×').

To describe the dependence of parameter c_I on the food concentration, ϕ, for filter-feeders, the classical Ivlev (1955) equation is often applied (cf. Sushchenya 1975):

$$(3) \quad \frac{dc_I}{d\phi} = \xi(c_{I\max} - c_I) \quad (\text{constants } c_{I\max}, \xi > 0).$$

The solution of the above equation is:

$$(4) \quad c_I(\phi) = c_{I,1}\{1 - \exp[-c_{I,2}(\phi + c_{I,3})]\} \quad (\text{constants } c_{I,1}, c_{I,2}, c_{I,3} > 0).$$

Agreement between this solution and our data is very good (see Fig. 1).

Food assimilation efficiency — In Table 3 are presented the instantaneous coefficients of food assimilation efficiency, U, calculated as follows (Grodzinski et al. 1975):

$$(5) \quad U = \frac{A}{C} = \frac{P + R}{C}$$

where C, A, R, P are the experimental instantaneous values of food consumption, assimilation, respiration, and total production, respectively. The coefficients calculated for the first, second, and third intervals in the female rotifer's life span do not provide any evidence of a systematic variation with age (see Table 3). Therefore, it is assumed in the model that U is independent of age for these three intervals, and equal to the experimental mean value. It is also assumed that U is not age-dependent for the mature female.

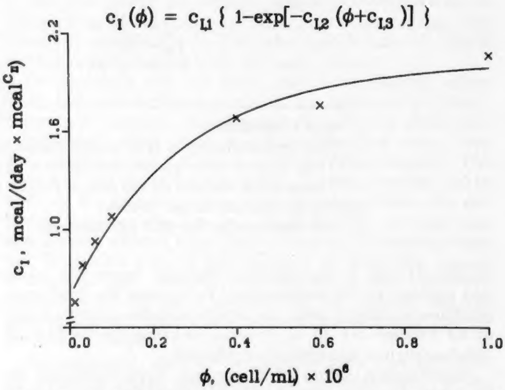

FIG. 1. Relation between the parameter c_I and the food concentration, ϕ. Symbol '×' — value of parameter c_I obtained by fitting function (2) to the experimental data (Table 1) using the mean value of the parameter c_{II}. Solid line — approximation by function (4) ($c_{I,1} = 2.0 \pm 0.1$; $c_{I,2} = 3.8 \pm 1.0$; $c_{I,3} = 0.09 \pm 0.03$).

In accordance with the above:

$$(6) \qquad U(\tau, \phi) = \begin{cases} U_{im}(\phi) \Leftrightarrow & 0 \leq \tau \leq \tau_m(\phi) \\ U_m(\phi) \Leftrightarrow & \tau_m(\phi) < \tau \leq \tau_L(\phi) \end{cases}$$

where $U_{im}(\phi)$, $U_m(\phi)$ are the instantaneous coefficients of food assimilation efficiency for the immature and mature female, respectively, $\tau_m(\phi)$ is the age at maturity, and $\tau_L(\phi)$ is the life span excluding a brief nonreproductive period preceding death. In reality, assimilation efficiency increases in a continuous way during maturation but since it changes rapidly over a short period of time, the above assumption (6) is permissible.

The instantaneous coefficients of assimilation efficiency for filter-feeders of a given body weight are assumed by Lehman (1976) to be dependent on the retention time of food in the digestive tract; the retention time is taken by Lehman (1976) to be inversely proportional to the instantaneous value of food consumption. In our model this latter value is directly proportional to the parameter c_I. Assuming that the relation between assimilation efficiency and retention time is linear we obtain:

$$(7) \qquad U_j(\phi) = u_{j,1} + \frac{u_{j,2}}{c_I(\phi)} \quad (\text{constants } u_{j,1}, u_{j,2} > 0)\, j = im, m.$$

We cannot verify separately each of the above assumptions on the basis of Pilarska's data, however we can state that function (7) approximates well the experimental relation between the food concentration and the mean value of food assimilation efficiency for the immature female rotifer (see Fig. 2).

Examination of the experimental P values for the mature female shows that they are undervalued. To prove this, we state first that for the mature female the following condition should be satisfied:

$$(8) \qquad \int_{\tau_m(\phi)}^{\tau_m(\phi)+\tau_e(\phi)} P(\tau, \phi)\, d\tau \geq W_o(\phi)$$

where $\tau_m(\phi)$ is the age at maturity, $\tau_e(\phi)$ is the interval between two successive acts of reproduction, and $W_o(\phi)$ is the egg calorific value. Pilarska's experimental P values for the mature female do not satisfy the above condition. As we discussed previously (see Experimental Measurements section) the undervaluation of P values for the mature female was likely due to the difficulty of measurement. It is known that the mature female rotifer produces eggs but does not grow when the food concentration is higher than 0.06 (cell/mL) × 10^6. This corresponds to the equality condition in (8) and enables us to replace the experimental values of total production for the mature female with values calculated from the equality condition utilizing the experimental values for W_o and τ_e (see Table 4).

If we assume that only the P values for the mature female were measured incorrectly, then we are able to estimate U, the instantaneous coefficients of assimilation efficiency, for the mature female on the basis of equation (5) by using experimental values for instantaneous food consumption, C, and respiration, R, but theoretical values for P from the equality in (8). These results are shown in Table 4. Estimation of the U-coefficients by this method is motivated by the greater accuracy of measurements of C, R, W_o, and τ_e than those of P.

The U-coefficients presented in Table 4 do not conform to the theoretical curve represented by equation (7). We have already noted that agreement between the curve and the experimental values for the immature female is very good; assuming that the relationship defined in the equation is also applicable for the mature female, we must conclude that the values presented in Table 4 are not completely correct. This leads us to suspect that another parameter, the interval between two successive acts of reproduction, $\tau_e(\phi)$, is not measured with enough accuracy for all investigated food concentrations. For each food concentration the interval $(\tau_L - \tau_m)$ should be close to an exact multiple of τ_e. This is not the case, suggesting that the values τ_e, τ_L, and τ_m might have considerable errors. The experimental calorific values for eggs, W_o, are not likely to be in error since the growth curves obtained from the model are in good agreement with the experimental data (see Validity of the Model section) and the initial values used in the model are the egg calorific values. The above discussion suggests that in order to deal with the case in which the mature female produces eggs but does not grow, we should determine new values for the instantaneous coefficients of assimilation efficiency of the mature female and also revise the values for the time interval between two successive acts of reproduction. We

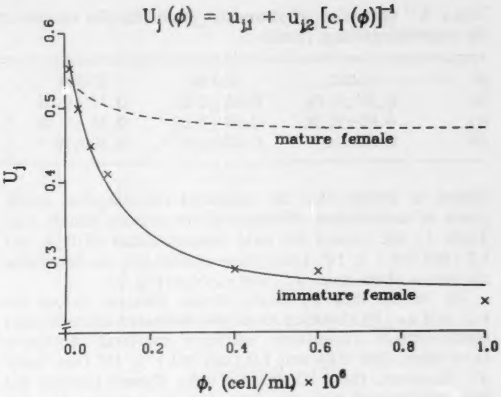

FIG. 2. Relation between the instantaneous coefficient of food assimilation efficiency, U, and the food concentration, ϕ. Symbol '×' — mean experimental coefficient for the immature female. Solid line — approximation by function (7) for the immature female ($u_{im,1} = 0.12 \pm 0.01$; $u_{im,2} = 0.29 \pm 0.01$). Dashed line — approximation by function (7) for the mature female ($u_{m,1} = 0.44$; $u_{m,2} = 0.06$).

TABLE 4. The instantaneous values of total production, P, evaluated on the basis of the equality in (8) and the instantaneous coefficients of food assimilation efficiency, U, calculated on the basis of formula (5) using P values from this table and C and R from Table 1. Presented values are for the mature female rotifer, at various constant food concentrations, ϕ.

ϕ	0.012	0.030	0.060	0.100	0.400	0.600	1.000
P	*	*	0.16	0.17	0.46	0.55	0.66
U	*	*	0.51	0.43	0.42	0.47	0.47

*It was impossible to estimate the value because of lack of reproduction for the majority of females at this food concentration.

TABLE 5. The values of parameters r_I and r_{II} (for various constant food concentrations, ϕ) obtained by fitting function (9) to the experimental data (Table 1).

ϕ	0.012	0.030	0.060	0.100	0.400	0.600	1.000
r_I	0.36 ± 0.03	0.36 ± 0.01	0.32 ± 0.01	0.32 ± 0.01	0.28 ± 0.01	0.29 ± 0.01	0.30 ± 0.02
r_{II}	0.60 ± 0.08	0.69 ± 0.03	0.65 ± 0.06	0.66 ± 0.05	0.79 ± 0.07	0.87 ± 0.08	0.89 ± 0.11
SS	0.22×10^{-3}	0.025×10^{-3}	0.10×10^{-3}	0.07×10^{-3}	0.11×10^{-3}	0.12×10^{-3}	0.22×10^{-3}

choose to assume that the estimated instantaneous coefficients of assimilation efficiency of the mature female (see Table 4) are correct for food concentrations of 0.06 and 1.0 (cell/mL) × 10^6. Using these coefficients, we determine the values of constants $u_{m,1}$ and $u_{m,2}$ (see Fig. 2).

We realize that we might obtain different values for $u_{m,1}$ and $u_{m,2}$ by choosing to use the estimated instantaneous coefficients of assimilation efficiency for food concentrations other than 0.06 and 1.0 (cell/mL) × 10^6 (see Table 4). However, these coefficients were chosen because (i) they correspond with the fact that, for mature females, the instantaneous coefficient of assimilation efficiency is a decreasing function of food concentration, and (ii) the food concentration of 1.0 (cell/mL) × 10^6 was of particular interest to the experimenter since it represents an optimal condition for the organism and therefore the experimental measurements are believed to be more reliable. We might expect that the values of U presented in Table 4 are not completely correct due to errors in the experimental values of C and R for the mature female. However, this is not very likely since the values of C and R for the mature female satisfy relations (2) and (9) which have been well verified for other species. Moreover, the use of values of $u_{m,1}$ and $u_{m,2}$ calculated as described above, necessitates only small corrections (in the range of the experimental errors) to the measured values of τ_e (see Egg Calorific Value, ... section). We recognize the fact that only further experimental studies can validate these assumptions regarding the mature female; and we recommend and specify such studies (see Suggestions for Further Studies section).

Respiration — Many investigators (cf. Brody 1945; Zeuthen 1953; Winberg 1956, 1966; Kleiber 1961; Prosser and Brown 1961; Duncan and Klekowski 1975) point out that the instantaneous value of respiration of an animal, in particular of a filter-feeder, is an increasing power function of its body weight. Such a relation also appears to be satisfactory in the present case if we replace the body weight by the body calorific value, but only for an organism which has relatively small variability in its calorific equivalent per unit body weight (Pilarska 1971). Accordingly:

$$(9) \quad R = r_I W^{r_{II}}.$$

Once again we point out that W in the right-side of the equation includes the calorific value of a developing egg if present. Pilarska's experimental data confirm relation (9). The values of parameters r_I and r_{II} for various constant food concentrations, obtained from fitting function (9) to the experimental data, as well as the sums of squares of residuals, SS, are presented in Table 5. The parameter r_{II} should be independent of the level of available food (cf. Paloheimo and Dickie 1965, 1966a, b). The values of r_{II} appear to increase with increasing food concentration, however considering the insensitivity of the model to changes in this parameter (see Sensitivity Analysis section) we choose to assume that the parameter r_{II} is independent of food concentration and is equal to the mean value of 0.74 ± 0.04.

Utilizing the mean value of parameter r_{II}, new values of parameter r_I for the various food concentrations are determined (Fig. 3, symbol '×') to obtain the best fit to experimental data.

The increase in the parameter r_I with decreasing food concentration can easily be explained by the increase in the energetic costs of filtration. If food resources are poor, the rotifer increases its filtration rate in order to satisfy the demand for energy. Therefore we should definitely take into account the relation between the parameter r_I and the filtration rate, f. It was assumed that for individuals having identical calorific values, the parameter r_I is a linear function of the filtration rate, f:

$$(10) \quad r_I = r'_{I,1} + r'_{I,2} f.$$

If f is to be measured in volume units per time units, we obtain the following relation (Pilarska 1971; Lehman 1976; Lam and Frost 1976):

$$(11) \quad f = \frac{1}{\phi q} \frac{dC_c}{d\tau}$$

where q is the calorific value of an alga cell. Taking into account the direct proportionality of the instantaneous value of food consumption to the parameter c_I, for individuals having identical calorific values, we obtain:

$$(12) \quad r_I(\phi) = r_{I,1} + r_{I,2}\, c_I(\phi) \cdot \phi^{-1} \text{ (constants } r_{I,1}, r_{I,2} > 0).$$

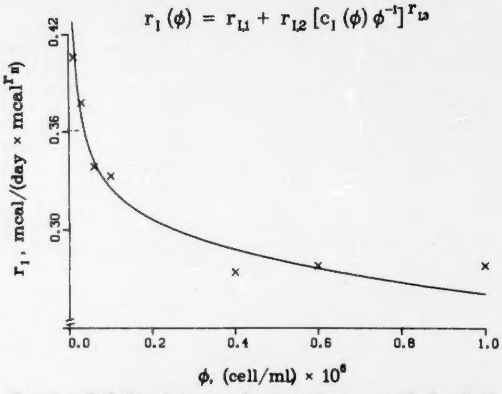

FIG. 3. Relation between the parameter r_I and the food concentration, ϕ. Symbol '×' — value of parameter r_I obtained by fitting function (9) to the experimental data (Table 1) using the mean value of the parameter r_{II}. Solid line — approximation by function (13) ($r_{I,1} = 0.10 \pm 0.07$; $r_{I,2} = 0.14 \pm 0.03$; $r_{I,3} = 0.20 \pm 2.35$).

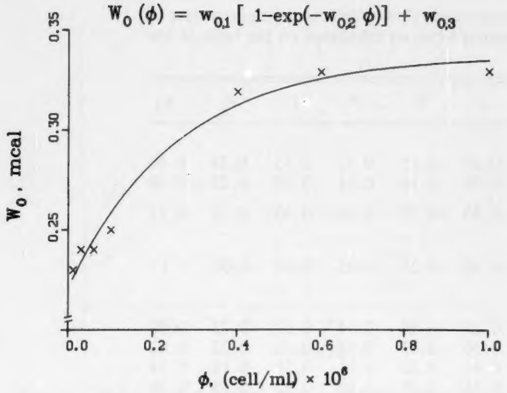

FIG. 4. Relation between the egg calorific value, W_o, and the food concentration, ϕ. Symbol '×' — experimental data. Solid line — approximation ($w_{o,1} = 0.117 \pm 0.009$; $w_{o,2} = 3.9 \pm 1.1$; $w_{o,3} = 0.221 \pm 0.007$).

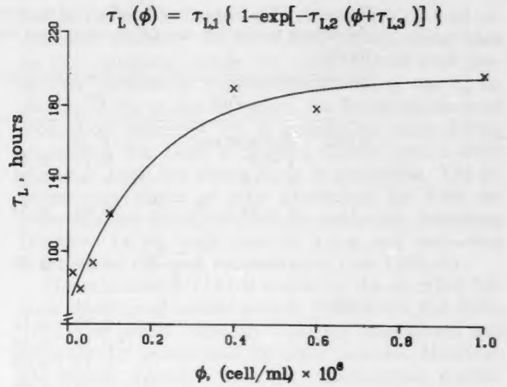

FIG. 6. Relation between the life span, τ_L, and the food concentration, ϕ. Symbol '×' — experimental data. Solid line — approximation ($\tau_{L,1} = 195. \pm 10.$; $\tau_{L,2} = 5.0 \pm 1.8$; $\tau_{L,3} = 0.09 \pm 0.04$).

This formula does not provide a very good approximation to the data presented in Fig. 3 (symbol '×'). With optimally chosen parameters, the sum of squares of residuals totalled 0.28×10^{-2}. Therefore the formula is modified so that

(13) $r_I(\phi) = r_{I,1} + r_{I,2}[c_I(\phi)\cdot\phi^{-1}]^{r_{I,3}}$

(constants $r_{I,1}, r_{I,2}, r_{I,3} > 0$).

This gives a good approximation to the data representing the relation between the parameter r_I and the food concentration (see Fig. 3). With optimally chosen parameters, the sum of squares of residuals is 0.73×10^{-3}.

Egg calorific value, age at maturity, life span, and frequency of reproduction — Considering the difficulties in finding a theoretical justification for the choice of functions to approximate the relations between food concentration and parameters such as egg calorific value, age at maturity and life span, we choose without theoretical rationale, empirical functions that approximate well the experimental data and have relatively few parameters (see Fig. 4–6).

The relation between food concentration and the length of the interval between acts of reproduction (Fig. 7) is obtained as follows. For each food concentration experimentally investigated (excluding the two lowest concentrations), values for the parameter τ_e are estimated which enable the model to simulate the situation in which the mature female produces eggs but does not grow. The formula used in the model (see Fig. 7) is chosen to obtain

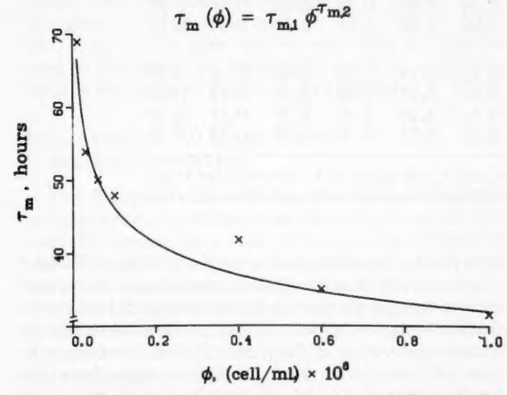

FIG. 5. Relation between the age at maturity of the female rotifer, τ_m, and the food concentration, ϕ. Symbol '×' — experimental data. Solid line — approximation ($\tau_{m,1} = 32.9 \pm 1.6$; $\tau_{m,2} = 0.16 \pm 0.02$).

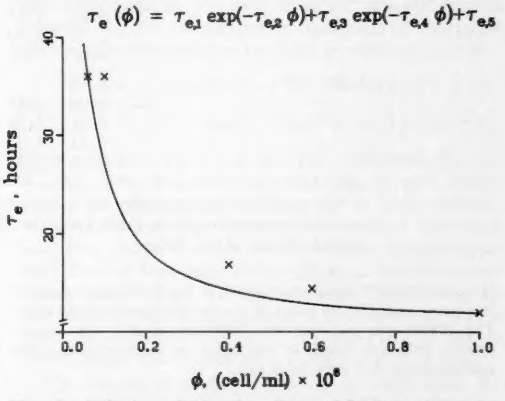

FIG. 7. Relation of the time interval between two successive acts of reproduction, τ_e, to the food concentration, ϕ. Symbol '×' — experimental data. Solid line — relation used in the model ($\tau_{e,1} = 12.55$; $\tau_{e,2} = 4.07$; $\tau_{e,3} = 43.62$; $\tau_{e,4} = 18.46$; $\tau_{e,5} = 11.75$).

TABLE 6. The body calorific value and the instantaneous values of bioenergetic parameters of the female rotifer (at various constant food concentrations, ϕ) calculated on the basis of the model.

ϕ	Age	W^a	C	A	R	P	U	K_1	K_2
0.012	diploidal egg	0.23							
	$\tau = 6$	0.29	0.49	0.27	0.15	0.12	0.55	0.24	0.44
	$\tau = 18$	0.34	0.51	0.28	0.18	0.11	0.55	0.22	0.39
	$\tau = 24 + \frac{\tau_m - 24}{2}$	0.48	0.54	0.30	0.22	0.08	0.55	0.15	0.27
	$\tau = \tau_m + \frac{\tau_L - \tau_m}{2}$	0.50	0.56	0.30	0.25	0.05	0.55	0.09	0.17
0.03	”	0.24							
		0.30	0.56	0.28	0.14	0.14	0.51	0.25	0.50
		0.37	0.59	0.30	0.17	0.13	0.51	0.22	0.43
		0.52	0.62	0.32	0.21	0.11	0.51	0.18	0.34
		0.59	0.66	0.35	0.25	0.10	0.52	0.15	0.29
0.06	diploidal egg	0.25							
	$\tau = 6$	0.33	0.67	0.30	0.14	0.16	0.45	0.24	0.53
	$\tau = 18$	0.40	0.71	0.31	0.16	0.15	0.45	0.21	0.48
	$\tau = 24 + \frac{\tau_m - 24}{2}$	0.56	0.75	0.33	0.20	0.13	0.45	0.17	0.39
	$\tau = \tau_m + \frac{\tau_e}{2}$	0.68	0.81	0.41	0.26	0.16	0.51	0.20	0.39
0.10	”	0.26							
		0.35	0.80	0.32	0.14	0.18	0.40	0.23	0.56
		0.43	0.85	0.33	0.16	0.17	0.40	0.20	0.52
		0.59	0.89	0.35	0.20	0.16	0.40	0.18	0.46
		0.72	0.96	0.48	0.26	0.23	0.50	0.24	0.48
0.40	”	0.31							
		0.44	1.37	0.39	0.14	0.25	0.29	0.18	0.64
		0.56	1.46	0.42	0.17	0.25	0.29	0.17	0.60
		0.70	1.53	0.44	0.21	0.24	0.29	0.16	0.55
		0.86	1.64	0.79	0.26	0.53	0.48	0.32	0.67
0.60	”	0.33							
		0.46	1.52	0.41	0.14	0.28	0.27	0.18	0.68
		0.60	1.62	0.44	0.17	0.27	0.27	0.17	0.61
		0.72	1.70	0.46	0.20	0.26	0.27	0.15	0.57
		0.88	1.81	0.86	0.25	0.61	0.48	0.34	0.71
1.00	”	0.34							
		0.48	1.63	0.43	0.13	0.29	0.26	0.18	0.67
		0.63	1.74	0.46	0.17	0.29	0.26	0.17	0.63
		0.73	1.81	0.48	0.19	0.28	0.26	0.15	0.58
		0.90	1.93	0.92	0.24	0.68	0.47	0.35	0.74

[a] For each food concentration, the second, third, and fourth values of W are evaluated at the end of the period defined in Table 1 and the fifth value is evaluated at the age indicated in the second column of this Table.

(i) a decrease in the parameter τ_e if the food concentration increases, and (ii) an exact fit to the estimated values of τ_e. The differences between the fitted curve and the experimental data are small, in the range of experimental error (estimated as 2–3 h by Pilarska).

Results and Discussion

VALIDITY OF THE MODEL

The model results conform well to the experimental data for the immature female rotifer (compare Tables 1 and 6, see also Fig. 8). Differences between the experimental data for the mature female rotifer and the results from the model, especially with reference to the instantaneous values of food assimilation, food assimilation efficiency, and total production have been discussed before.

From the growth curves (Fig. 8), the body calorific value excluding eggs is seen to be a strictly increasing function of the food concentration at any given age.

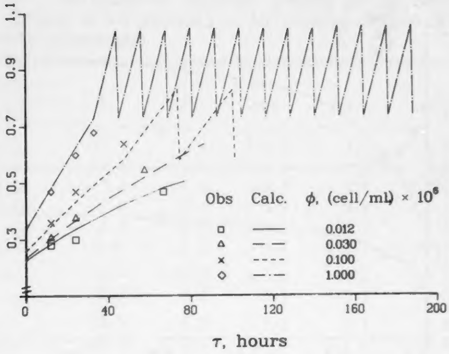

FIG. 8. Relation between the body calorific value of the female rotifer, W, and its age, τ, at various constant food concentrations, ϕ.

This is in agreement with experimental observations.

Growth curves for food concentrations in the range of 0.4–1.0 (cell/mL) × 10^6 are quite similar; moreover, throughout this range the cumulative bioenergetic parameters (to be discussed in Instantaneous Coefficients . . . section) are close to their asymptotic values. In other words, food concentration is not a factor in energy flow through the female rotifer, if it falls within the range described above.

Simulation of the energy flow through this organism at food concentrations higher than 1.0 (cell/mL) × 10^6 does not produce biologically meaningful results because in nature, food concentrations higher than this level produce unfavorable changes in the rotifer's environment (see Pilarska 1971, 1977a, b, c) and these changes are not taken into account in the model. The lowest food concentration at which the female rotifer can grow is 0.012 (cell/mL) × 10^6 (Pilarska 1971, 1977a, b, c). To sum up, we state that all relations used in the model are biologically valid for concentrations in the range of 0.012 to 1.0 (cell/mL) × 10^6.

INSTANTANEOUS VALUES OF ENERGY BALANCE PARAMETERS

The changes in the instantaneous value of food consumption due to different food concentrations are considerably greater than those which can be attributed to variability in W at a given value of ϕ (see Table 6). For the other instantaneous energy balance parameters, A, R, and P, this is not the case; their range of changes attributable to the variability of W for a given value of ϕ is comparable to that due to the range of ϕ values.

Instantaneous value of total production, P, is determined according to the model as follows:

$$(14)\quad P = \begin{cases} U_{im} c_I W^{c_{II}} - r_I W^{r_{II}} \Leftrightarrow 0 \leq \tau \leq \tau_m \\ U_m \cdot c_I W^{c_{II}} - r_I W^{r_{II}} \Leftrightarrow \tau_m < \tau \leq \tau_L. \end{cases}$$

Due to the higher instantaneous coefficient of food assimilation efficiency for the mature female rotifer than for the immature female, the instantaneous total production increases in a discontinuous way at age τ_m according to the model. In reality, the instantaneous total production increases in a continuous way during maturation but since it changes rapidly over a short period of time, the above result is acceptable. The instantaneous values of total production for both the immature and the mature female rotifer are decreasing functions of its body calorific value and increasing functions of the food concentration (see Table 6).

The relationship (14) is similar to the so-called balance equation of animal growth (Makarova and Zaika 1971), originally assumed valid for crustaceans and subsequently generalized for other animals. However, the balance equation describes instantaneous production excluding reproductive products while the above equation includes these products. Furthermore, Makarova and Zaika use the body weight excluding reproductive products in the right-hand side of the equation instead of the body calorific value. They also assume the instantaneous coefficient of food assimilation efficiency to be totally independent of the animal's age.

INSTANTANEOUS COEFFICIENTS OF ENERGY CONVERSION EFFICIENCY

Equations (2) and (14) allow us to find the relation between K_1, the instantaneous coefficient of utilization of the consumed energy for total production, and W, the body calorific value of the female rotifer:

$$(15)\quad K_1 = \frac{P}{C} = \begin{cases} U_{im} - r_I c_I^{-1} W^{(r_{II} - c_{II})} \Leftrightarrow 0 \leq \tau \leq \tau_m \\ U_m - r_I c_I^{-1} W^{(r_{II} - c_{II})} \Leftrightarrow \tau_m < \tau \leq \tau_L \end{cases}$$

and using equation (6) as well we can find the relation between K_2, the instantaneous coefficient of utilization of the assimilated energy for total production, and W:

$$(16)\quad K_2 = \frac{P}{A} = \begin{cases} 1 - r_I (c_I U_{im})^{-1} W^{(r_{II} - c_{II})} \Leftrightarrow 0 \leq \tau \leq \tau_m \\ 1 - r_I (c_I U_m)^{-1} W^{(r_{II} - c_{II})} \Leftrightarrow \tau_m < \tau \leq \tau_L. \end{cases}$$

These relations point out that the coefficients K_1 and K_2 for both the immature and the mature female rotifer are decreasing functions of its body calorific value and increasing functions of the food concentration (see Table 6). Due to the higher instantaneous coefficient of food assimilation efficiency for the mature female rotifer than for the immature female, the coefficients K_1 and K_2 increase in a discontinuous way at age τ_m according to formulas (15) and (16). In reality, this increase takes place over a brief period of time.

We observe that the variability in coefficients K_1, K_2, and U attributable to the variability in W for a given value of ϕ is comparable to that due to the range of ϕ values.

The instantaneous coefficients K_1 and K_2 for the immature female, calculated on the basis of Pilarska's

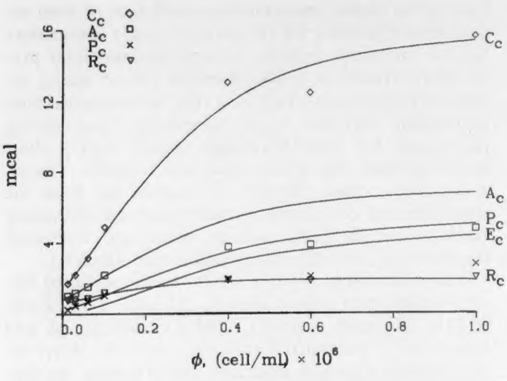

FIG. 9. Relation between the values of food consumption, C_c, food assimilation, A_c, total production, P_c, egg production, E_c, respiration, R_c, cumulated over the rotifer's life span, and food concentration, ϕ. Solid line — curve obtained from the model; symbols — values obtained by Pilarska (1977c) on the basis of direct estimation.

data, confirm relations (15) and (16). K_1 and K_2 for the mature female (Table 6), calculated on the basis of formulas (15) and (16) are higher than the experimental ones (Pilarska 1971, 1977c). The reasons for this were presented previously.

The Winberg equation and its interpretation, which is postulated (Winberg 1966) for the general case, lead to the following relation between the instantaneous coefficient of utilization of the assimilated energy for body growth, $K_2(\tilde{K}_2 = (d\tilde{W}/d\tau)/A)$, and the calorific value of the body excluding eggs, $\tilde{W}$:

$$(17) \quad \tilde{K}_2 = \frac{H\tilde{W}^{r_{II}} - K\tilde{W}}{(r_I + H)\tilde{W}^{r_{II}} - K\tilde{W}}$$

where H and $\tilde{K}$ are constants of the Winberg equation. The coefficient $\tilde{K}_2$ should be equal to the coefficient K_2 up to maturity because the total production for this period is equal to the increase in the body calorific value. Despite the difference between formulas (16) and (17), it is difficult to state without further study whether or not the Winberg equation and its interpretation are valid in the case of the amictic female rotifer *B. rubens*. It is quite possible that two different functions can approximate the same experimental relation (Majkowski and Uchmanski 1980).

The comparison between the instantaneous coefficients of energy conversion efficiency of the amictic female rotifer *B. rubens* and other animals is made by Pilarska (1971, 1977c).

CUMULATIVE VALUES OF BIOENERGIC PARAMETERS

Values of food consumption, C_c, food assimilation, A_c, total production, P_c, egg production, E_c, and respiration, R_c, for the female rotifer, cumulated over its life span, τ_L, as functions of the food concentration, are presented in Fig. 9.

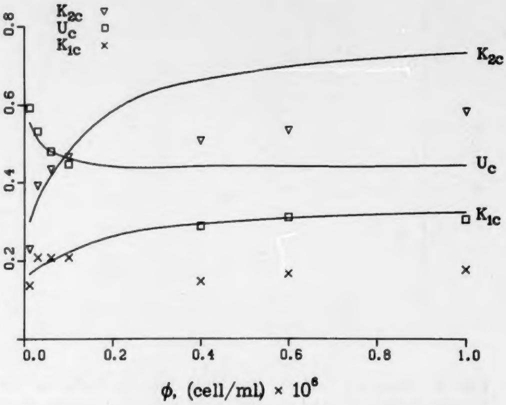

FIG. 10. Relation between the cumulative coefficients of energy conversion efficiency K_{2c}, U_c, K_{1c}, and the food concentration, ϕ. Solid line — curve obtained from the model; symbols — values obtained by Pilarska (1977c) on the basis of direct estimation.

Cumulative coefficients such as those for assimilation efficiency, U_c ($U_c \equiv A_c/C_c$), utilization of consumed energy for total production, K_{1c} ($K_{1c} \equiv P_c/C_c$), and utilization of assimilated energy for total production, K_{2c} ($K_{2c} \equiv P_c/A_c$), for the female rotifer, as functions of the food concentration, are presented in Fig. 10.

There are substantial differences between the curves from the model (Fig. 9 and 10) and the values obtained by Pilarska (1977c) on the basis of direct estimation in the case of some cumulative parameters. Pilarska's values for food assimilation, total production and coefficients of energy conversion efficiency are lower than those calculated on the basis of the model. This, we have argued, is a result of incorrect measurement of the instantaneous value of total production for the mature female. The results obtained with the aid of the model indicate that the amictic female rotifer *B. rubens* has a higher efficiency of energy conversion than was originally assumed (Pilarska 1977c). The curves from the model (see Fig. 9 and 10) are close to their asymptotic values when the value of food concentration is about 0.4 (cell/mL) × 10^6.

Comparisons between the cumulative values of bioenergetic parameters of the amictic female rotifer *B. rubens* and other animals are available in Pilarska's papers (1971, 1977c).

SENSITIVITY ANALYSIS

Examination of the performance of the model when its parameters are slightly changed is called sensitivity analysis (cf. Tomovic 1963; Kowal 1971; Waide and

TABLE 7. The results of sensitivity analysis for the food concentration of 1.0 (cell/mL) × 10^6 (relative changes expressed as percentages).

Perturbed parameter	ΔW_c	ΔP_c	ΔC_c	ΔA_c	ΔR_c
$c_{I(m)}$	22.2	4.1	4.6	4.8	6.9
$U_{(m)}$	22.2	4.1	1.9	4.8	6.9
$r_{I(m)}$	−5.8	−1.1	−0.5	−0.6	0.8
$c_{I(im)}$	2.4	0.4	0.9	0.7	1.6
$U_{(im)}$	2.4	0.4	0.5	0.7	1.6
$r_{I(im)}$	−0.9	−0.2	−0.2	−0.2	−0.2
c_{II}	−0.9	−0.2	−0.2	−0.2	−0.4
r_{II}	0.8	0.2	0.1	0.1	0.0
τ_L	18.3	3.3	3.1	3.3	3.4
W_{oe}	−16.2	−0.3	−1.5	−1.6	−4.9
τ_e	1.0	0.2	1.4	1.5	5.1
τ_m	−2.1	−0.4	−0.4	−0.6	−1.3
W_{oi}	1.3	0.0	0.3	0.3	0.9

Webster (1976). The procedure points out parameters which, if changed, produce either strong or weak changes in the output from the model. This analysis provides some information as to the direction in which further experimental and theoretical studies should proceed.

Sensitivity analysis was performed for a few fixed food concentrations. One after another, the value of each parameter was increased by 3%. Parameters which are directly proportional to the instantaneous values of food consumption, food assimilation and respiration (i.e. c_I,[3] U, r_I) were increased separately for the periods of immaturity (denoted in the table by *im*) and of maturity (denoted by *m*). The effects of such changes on the performance of the model were determined by the relative changes (expressed as percentages) in the values of energy balance parameters cumulated over the life span (ΔC_c, ΔA_c, ΔR_c, ΔP_c), and by the relative changes in the body calorific value of the female rotifer at the end of its life span (ΔW_c). The results of sensitivity analysis for a food concentration of 1.0 (cell/mL) × 10^6 are presented in Table 7.

These results vary with food concentration. The model displays high sensitivity to changes for the period of maturity in the parameters c_I and U when the supply of food is plentiful. As the amount of available food decreases the model gradually becomes most sensitive to changes for the period of immaturity in c_I and U.

Regardless of food concentration then, the model is very sensitive to changes in (listed in order of importance): the instantaneous value of food consumption, food assimilation efficiency, the life span and the egg calorific value. The model is relatively insensitive to changes in the initial body calorific value, the age at maturity, the time interval between two successive acts of reproduction and the instantaneous value of respiration.

Suggestions for Further Studies

1) Measurements of parameters characterizing an organism which change during its life span should all be taken at the same age intervals. If possible measurements should be taken most frequently in the periods during which the parameters are changing rapidly. It would be helpful to determine the experimental errors of all measured parameters, in order to allow for internal model validation (Miller 1974; Miller et al. 1976).

2) The accuracy with which each parameter is measured should be proportional to the degree of sensitivity displayed by the model to changes in that parameter. We emphasize this recommendation in the consideration of three bioenergetic parameters: food consumption, food assimilation efficiency and respiration. Based on the structure of the general model of energy flow through an animal organism (Majkowski 1978) and on sensitivity analysis for the female rotifer as well as for the female crustacean *Simocephalus vetulus*. (Majkowski 1978; Klekowski and Majkowski 1980) and the female root mite *Rhizoglyphus echinopus* (Klekowski and Uchmański 1980) we conclude that for any animal the relative accuracy of measurement of the first two parameters needs to be much better than the relative accuracy of measurement of the third. This should be an important consideration in bioenergetic studies in general since experimental methods for measuring respiration are, in many cases, more advanced than those for food consumption, assimilation and assimilation efficiency (Grodzinski et al. 1975).

3) It is desirable to obtain new measurements for the bioenergetic parameters of the mature female rotifer *B. rubens* bearing in mind the recommendations given above. Also, the time interval between two successive reproductive acts and the egg calorific value should be measured once again. In the present model it is assumed that the instantaneous value of food consumption is a power function of the body calorific value including eggs. There is a second possibility: a power function of the body calorific value excluding eggs. The first assumption results in a constant instantaneous value of total production for the period of maturity, which is reasonable. The second assumption implies a decreasing instantaneous value of total production in the period between two successive acts of reproduction, a situation which is not likely from the biological point of view. Nevertheless the assumption utilized in the model should be verified experimentally.

4) The present model indicates that an increase in filtration rate at a constant food concentration increases the instantaneous value of food consumption and respiration and decreases the instantaneous coefficient of food assimilation efficiency. The cost of digestion, on the basis of the model, is largely independent of the

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[3] c_I was increased only in formula (2).

instantaneous value of food consumption. The filtering response of filter-feeders to changes in food concentration was explained by Lehman (1976) and Lam and Frost (1976) under the assumption that the instantaneous value of total production is maximized. The models developed by Lehman and Lam and Frost are formulated on the basis of hypothetical physical assumptions rather than experimental data. It would be interesting to check the validity of their assumptions in the light of relations derived from a model constructed on the basis of biological data and also to examine whether or not the female filter-feeder adjusts its filtration rate at each food concentration level to maximize the value of egg production, cumulated over its life span.

Relation (13) implies that the cost of filtration is an increasing power function of the filtration rate. Lehman (1976), Lam and Frost (1976) used a similar form for this relation in their models based on an analogy to a physical mechanism of liquid flow. However, their power value was greater than one while ours is not ($r_{I,8} = 0.20 \pm 2.35$). Although our value is apparently subject to enormous estimation error, Pilarska's biological data suggest that $r_{I,8}$ should be less than one. The collection of additional data for the rate of respiration could help in making a final judgement regarding the true value for this parameter. Since the power value largely determines the strategy of filtration, such a study would seem to be important to the understanding of the bioenergetics of filter-feeders.

5) The present model simulates energy flow through the female rotifer at various food concentrations (in the range of 0.012–1.0 (cell/mL) × 10^6) which remain constant during the rotifer's life span. It would be interesting to develop a model which would provide biologically correct results for changing food concentrations. Relatively few growth models do provide biologically correct results for changing environmental conditions (see review, Majkowski and Uchmański 1980). Such a model would provide a better understanding of the energy economy of the organism being studied and furthermore, it could be used in developing simulations of complex ecological systems (e.g. Majkowski 1977). The latest theory on population dynamics (Lomnicki 1978) emphasizes differences among animals' individual growth patterns as an important factor in the natural regulation of the number of individuals. This new emphasis should stimulate the development of growth models.

Acknowledgments

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Glossary

Symbol	Unit	Description
A_c	mcal	value of food assimilation cumulated over the age interval $[0, \tau]$
c_I, c_{II}	*	parameters of the function approximating the relation between the instantaneous value of food consumption and body calorific value ($C = c_I W^{c_{II}}$)
$c_{I\max}$	*	parameter of the Ivlev equation
$c_{I,1}$, $c_{I,2}$, $c_{I,3}$	*	constants of the function approximating the relation between the parameter c_I and food concentration
C	mcal·d^{-1}	instantaneous value of food consumption
C_c	mcal	value of food consumption cumulated over the age interval $[0,\tau]$
E_c	mcal	value of egg production cumulated over the age inverval $[0, \tau]$
f	mL·d^{-1}	filtration rate
H	*	parameter of the Winberg equation
K	*	parameter of the Winberg equation
K_1	—	instantaneous coefficient of utilization of consumed energy for total production ($K_1 = P/C$)
K_2	—	instantaneous coefficient of utilization of assimilated energy for total production ($K_2 = P/A$)
$\bar{K}_2$	—	instantaneous coefficient of utilization of assimilated energy for body growth $\left(\bar{K}_2 = \frac{d\bar{W}}{d\tau} \Big/ A\right)$
K_{1c}	—	cumulative coefficient of utilization of consumed energy for total production ($K_{1c} = P_c/C_c$)
K_{2c}	—	cumulative coefficient of utilization of assimilated energy for total production ($K_{2c} = P_c/A_c$)
n	—	number of eggs laid to age τ
P	mcal·d^{-1}	instantaneous value of total production
P_c	mcal	value of total production cumulated over the age inverval $[0, \tau]$
q	mcal	calorific value of an alga cell
r_I, r_{II}	*	parameters of the function approximating the relation between the instantaneous value of respiration and body calorific value ($R = r_I W^{r_{II}}$)

$r_{I,1}, r_{I,2}, r_{I,3}$	*	constants of the function approximating the relation between the parameter r_I and food concentration
R	$\mathrm{mcal \cdot d^{-1}}$	instantaneous value of respiration
R_c	mcal	value of respiration cumulated over the age interval $[0, \tau]$
U	—	instantaneous coefficient of food assimilation efficiency $(U = A/C)$
U_c	—	cumulative coefficient of food assimilation efficiency $(U_c = A_c/C_c)$
$u_{j,1}, u_{j,2}$	—	constants of the function approximating the relation between the instantaneous coefficient of food assimilation efficiency and food concentration
W	mcal	calorific value of the female body including eggs
W	mcal	calorific value of the female body excluding eggs
W_c	mcal	calorific value of the female body at the end of its lifespan
W_o	mcal	egg calorific value
W_{oe}	mcal	calorific value of an egg (used in the section devoted to sensitivity analysis)
W_{ot}	mcal	initial body calorific value (used in the section devoted to sensitivity analysis)
$w_{o,1}, w_{o,2}, w_{o,3}$	*	constants of the function approximating the relation between the egg calorific value and food concentration
Δ	%	the relative change in a parameter, e.g. $\Delta P_c = 100[P_c - P_c)/P_c]$ where P_c is the value of total production cumulated over the age interval $[0, \tau_L]$ when a selected parameter of the model is increased by 3%; P_c is the value of total production cumulated over the age interval $[0, \tau_L]$ from the unperturbed run of the model (this refers to the sensitivity analysis section)
ϕ	$(\mathrm{cell/mL}) \times 10^6$	food concentration
τ	days or hours	age of the female
τ_e	hours	time interval between two successive acts of reproduction
$\tau_{e,1}, \tau_{e,2}, \tau_{e,3}, \tau_{e,4}, \tau_{e,5}$	*	constants of the function approximating the relation between time τ_e and food concentration
τ_L	hours	average life span excluding a brief nonreproductive period preceding death
$\tau_{L,1}, \tau_{L,2}, \tau_{L,3}$	*	constants of the function approximating the relation between τ_L and food concentration
τ_m	hours	age at maturity
$\tau_{m,1}, \tau_{m,2}$	*	constants of the function approximating the relation between age at maturity and food concentration
ξ	*	parameter of the Ivlev equation

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*These parameters have no simple biological meaning and the units are very complicated; hence they are not presented.

NOTES

A Simple Reflectance Method for the Measurement of Particulate Pigment in Lake Water and its Application to Phosphorus–Chlorophyll–Seston Relationships[1]

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BERGMANN, M., AND R. H. PETERS. 1980. A simple reflectance method for the measurement of particulate pigment in lake water and its application to phosphorus–chlorophyll–seston relationships. Can. J. Fish. Aquat. Sci. 37: 111–114.

This paper describes a new method to measure total sestonic pigment based on the reduction in the amount of light reflected from a membrane filter after a given volume of lake water has passed through the filter. For a sample of 30 lakes, this index of "reflectance" gave a better regression on total phosphorus than did chlorophyll which suggests that part of the variation in published phosphorus–chlorophyll relationships results from the association of phosphorus with pigments other than chlorophyll. But the residual variation suggests both that the amount of pigment developed per unit of phosphorus varies among lakes and that the index does not completely represent the seston. Relationships between reflectance and concentration of chlorophyll, phosphorus, and seston are good enough to suggest that this rapid, easy analysis may find application as an adjunct to more traditional analyses whereever membrane filters are routinely used in the analysis of lake water.

Key words: Total pigment analysis, seston, phosphorus–chlorophyll

BERGMANN, M., AND R. H. PETERS, 1980. A simple reflectance method for the measurement of particulate pigment in lake water and its application to phosphorus–chlorophyll–seston relationships. Can. J. Fish. Aquat. Sci. 37: 111–114.

Le présent article décrit une nouvelle méthode de détermination du pigment sestonique total fondée sur la diminution de la quantité de lumière réfléchie depuis un filtre à membrane après qu'un volume donné d'eau de lac ait traversé le filtre. Sur un échantillon de 30 lacs, on obtient, grâce à cet indice de «réflectance», une meilleure régression sur le phosphore total qu'avec la chlorophylle. Ceci donne à penser qu'une partie de la variation des relations phosphore–chlorophylle publiées résulte de l'association du phosphore avec des pigments autres que la chlorophylle. Par ailleurs, la variation résiduelle suggère à la fois que la quantité de pigment formé par unité de phosphore varie d'un lac à l'autre et que l'indice ne représente pas complètement le seston. Les relations entre la réflectance et la concentration de chlorophylle, de phosphore et de seston sont suffisamment bonnes pour que cette analyse, facile et rapide, trouve application comme supplément aux analyses traditionnelles quand on utilise de façon routinière des filtres à membrane dans l'analyse de l'eau de lac.

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EMPIRICAL relationships between seasonally averaged concentrations of total phosphorus and chlorophyll *a* have proven a powerful tool in lake management (Dillon and Rigler 1974a). Nevertheless, for any published correlation, the confidence limits around predicted chlorophyll *a* concentration are broad (Dillon and Rigler 1974b) and differences among published relationships are considerable. Nicholls and Dillon (1978) believe a part of the scatter arises because chlorophyll *a* is an inadequate estimator of both algal and seston concentration; they found that total cell volume correlates better with total P concentration than does chlorophyll *a*. Unfortunately, the measurement of cell volume demands both expertise and labor. A method to estimate total pigment could prove a useful alternative to both chlorophyll *a* analysis and cell volume measurements: faster and simpler than the latter, but a

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more adequate index of total seston than the former.

When lake water is passed through a membrane filter, the surface of the filter becomes discolored. Vallentyne et al. (1970) noted that the degree of discoloration appears proportional to the concentration of phosphate and seston, in the water; they proposed that such filters could serve as a qualitative, visual index of eutrophy. We here describe a method in which this index is quantified by measuring light reflected from the filter's surface. Subsequently values of this index, "reflectance," were measured for a series of lakes in Ontario and Quebec to determine if such a measure of total seston yields a better regression against total phosphorus than does chlorophyll concentration. Such a result would indicate that a part of the variation in phosphorus–chlorophyll relationships results from the association of P with nonalgal, or at least, nonchlorophyll elements in the seston. The data are then used to show that predictive relationships exist between reflectance and total phosphorus, chlorophyll concentrations, and dry weight of seston.

Materials and methods — To measure reflectance, we directed a beam of defined light onto a filter and measured, photometrically, the amount of light reflected from the filter's surface. The light source was a Carl Zeiss 6V 15W bench illuminator set at 5.0 V and equipped with a neutral blue filter, a vertical polarizing lens and a 12% neutral density filter. The neutral blue filter served to bring the light quality to daylight standards by compensating for the spectral disproportion in light emitted by the tungsten illuminator. Light was polarized to minimize glare from any crystalline structures on the filters. Neutral density filters were used to reduce the light intensity. The incident light beam was directed, at an angle of 45°, to the surface of a 47-mm diameter, 0.45-μm porosity HA Millipore membrane filter which was held flat to a horizontal mat black surface by the weight of a metal bracket. The reflected beam was measured with an electronic exposure photometer (Photovolt Corporation, New York, Model 520A). The light sensor, a 2.5-cm diameter photocell was fitted with a 3% neutral density filter and a black collecting cone (length = 50 mm; aperture diameter = 10 mm) which reduced the effects of stray light. The cone and photocell were set at 90° to, and in the plane of, the incident beam and adjusted to maximize the amount of light collected. All measurements were performed in a photographic darkroom to reduce the effects of any stray light. Maximum values were determined by measuring the light reflected from an unused filter; maximum values were determined when the light source was turned off. These were used to calculate reflectance from a sample filter as a percentage of this range:

$$\text{Reflectance} = 100 \times \frac{\text{Reading from used filter} - \text{Reading from dark illuminator}}{\text{Reading from clean filter} - \text{Reading from dark illuminator}}$$

High values of reflectance should therefore indicate low concentrations of seston.

To evaluate this index as a measure of seston concentration, we prepared a series of standard filters. Aliquots (50–250 mL) of a rich algal suspension were passed through 47-mm diameter, 0.45-μm membrane filters. The filters were allowed to dry at room temperature in the laboratory, and their reflectance measured. Figure 1 shows that reflectance adequately represented the amount of material on each filter ($r^2 = 0.998$).

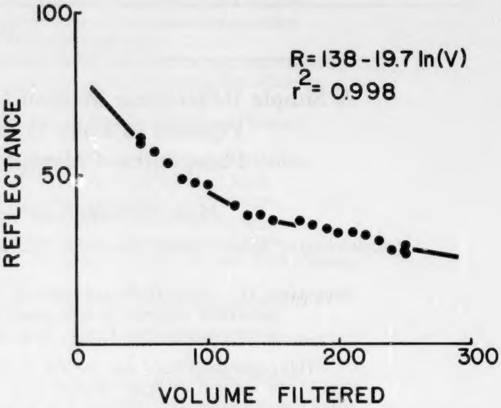

FIG. 1. Reflectance (R) from the surface of membrane filters obtained by filtering different volumes (V, in mL) of a dense algal culture.

The applicability of this technique to natural waters was examined with 2-L epilimnetic samples taken from 30 lakes and ponds in eastern Ontario and southwestern Quebec in July and August 1978. These samples were analyzed for reflectance, dry weight of seston, chlorophyll *a*, and total phosphorus concentration. When possible 250 mL of lake water were passed through a filter and the reflectance measured as described above. On two occasions when the filters clogged before 250 mL could be passed, a smaller volume was filtered and the reflectance standardized to 250 mL using the equation in Fig. 1. Filters were analyzed within 1 wk. Of these filters, 25 were stored in Glassine envelopes at room temperature until January 1979. Their reflectance was then measured again to indicate the effect of storage on the reflectance values. Total phosphorus, in replicate 50-mL aliquots of each sample, was measured using the ascorbic acid modification of the molybdenum blue reaction (Strickland and Parsons 1968) following oxidation, under pressure, with potassium persulphate (Menzel and Corwin 1965). Seston weight was determined by passing 15–100 mL of lake water through prewashed, dried, and preweighed 0.45 μm, 25-mm membrane filters which were then redried at room temperature and reweighed. Chlorophyll concentration was measured using the following ethanol extraction procedure developed by M. Ostrovsky (Biology Department, Alleghany College, Meadville, Penn.): 75–500 mL of lake water were passed through a glass fiber filter. If necessary the filter was then frozen and stored for up to 1 wk. Fresh or frozen filters were each placed in 10 mL of 95% ethanol, shaken initially and again after 1 h, and left overnight in a refrigerator. After this extraction, the ethanol was filtered and the optical density (OD) of the filtrate measured in a 10-cm cell using a Bausch and Lomb Spectronic 100 spectrophotometer set at 750, 655, and 649 nm. Chlorophyll *a* concentration in

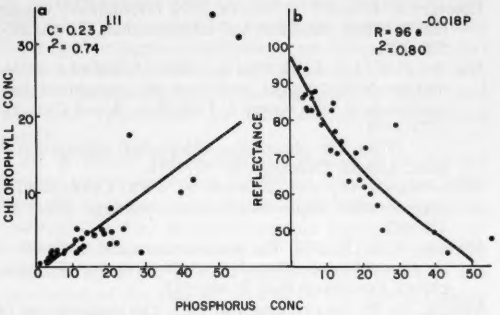

FIG. 2. Relationships between total phosphorus concentration (P, in $mg \cdot m^{-3}$) and 2a chlorophyll *a* concentration (C in $mg \cdot m^{-3}$); and 2b reflectance.

mg/m^3 is then calculated as:

$$\frac{13.7\,(OD_{665} - OD_{750}) - 5.76\,(OD_{649} - OD_{750})v}{V \cdot 10}$$

where v is the volume of extractant and V is the number of litres of lake water filtered. M. Ostrovsky (personal communication) has found that this procedure offers similar advantages to methanol extraction (Holm-Hansen and Riemann 1978), including easier and more complete extraction than achieved with more popular acetone extractions (Marker 1972).

Results and discussion — Figure 2 compares the relationship of total phosphorus concentration with chlorophyll (Fig. 2a) and with reflectance (Fig. 2b). The geometric mean or functional modification of least-squares analysis (Ricker 1973) was used to determine the equations in all figures. The phosphorus–chlorophyll relationship falls in the middle of the range of the various relationships collected by Nicholls and Dillon (1978). This demonstrates that our chlorophyll technique and the range of lakes studied can be considered representative. Regression of the natural logarithm (ln) of reflectance against total phosphorus yielded the highest correlation coefficient ($r^2 = 0.80$) of several transformations (linear, semilogarithmic, exponential, and double logarithmic). This regression explained more variation than the phosphorus–chlorophyll relationship ($r^2 = 0.74$) and deviations of the untransformed data from the curve were smaller (cf Fig. 2a and 2b). This suggests that total phosphorus is more closely related to this measure of total seston than to a measure of chlorophyll. Nevertheless, much more variation exists around the regression line than in the control experiment (Fig. 1). This was to be expected because reflectance can only be considered a partial index of seston concentration and because the amount of pigment developed depends on factors other than total phosphorus (Nicholls and Dillon 1978).

Regressions were also performed to produce predictive relationships for total phosphorus, chlorophyll, and seston weight on the basis of reflectance (Fig. 3). In each case, the highest correlation coefficients were obtained with a logarithmic transformation of one axis, and only those relations with the highest correlation coefficients are shown in Fig. 3. These regressions give a better fit to the data than predictive relations based on total phosphorus (Fig. 2; ln phosphorus vs. ln seston, $r^2 = 0.49$; phosphorus vs. seston, $r^2 = 0.55$). Because Ricker's (1973) model was used to describe all relationships, the relation predicting phosphorus from reflectance can be obtained by transposing the equation in Fig. 3b:

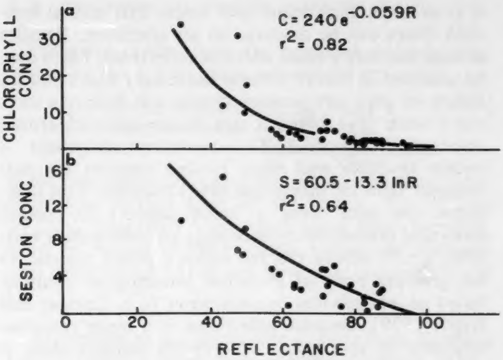

FIG. 3. Relationship between reflectance (R) and (3a) chlorophyll (C in $mg \cdot m^{-3}$) and (3b) dry weight of seston (S, in $g \cdot m^{-3}$).

$$P = 250 - 55 \ln R.$$

Regressions involving seston dry weight were consistently low probably because seston weights were small relative to variations in the weight of an individual membrane filter. However, of the two measures, total phosphorus and reflectance, reflectance yielded the better correlation to both seston and chlorophyll.

Finally, we examined changes in reflectance from 25 of the filters after 6 mo storage. A sign test (Conover 1971, p. 121) showed that there was a significant tendency for reflectance to increase in storage although the average increase was only 3.1 reflectance units (SE = 1.2). Regression analysis of the January data against total phosphorus yielded the relationship $P = 295 - 65 \ln R$ ($r^2 = 0.59$) which is scarcely different from that obtained using reflectance from the same 25 filters measured within a week of collection, $P = 291 - 64 \ln R$ ($r^2 = 0.74$), although the scatter was increased. Storage resulted in a statistically significant but practically unimportant loss of color.

We do not intend that reflectance measurements should replace total phosphorus or chlorophyll measurements. However, the measurement of reflectance does offer some very real advantages over other measures.

It is so exceedingly rapid and simple that several hundred filters can be analyzed in an afternoon. Because storage has only a small effect on reflectance, filters may be analyzed at leisure without the danger that a sudden failure in one's refrigeration system will destroy a summer's work (this is not a rare occurrence with frozen chlorophyll samples.) The necessary equipment is widely available and many routine analyses for particulates yield the membrane filters required. This technique can thus form a useful adjunct to current analytical procedures by providing an independent variable, which relates the researcher's prime interest to the growing body of empirical limnological relations based on phosphorus concentration (e.g. Cornett and Rigler 1979). Because reflectance is a more complete estimator of seston than chlorophyll concentration, it may prove a more adequate measure of suspended resources for models dealing with ingestion and secondary production processes in lakes.

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Analysis of Double-Tagging Experiments: An Update

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RUSSELL, H. J. JR. 1980. Analysis of double-tagging experiments: an update. Can. J. Fish. Aquat. Sci. 37: 114–116.

A mathematically corrected version of a previously published method for analyzing results of double-tagging experiments is presented. Analytical procedures are exemplified using lobster tag return data.

Key words: Double-tagging, analysis, update

RUSSELL, H. J. JR. 1980. Analysis of double-tagging experiments: an update. Can. J. Fish. Aquat. Sci. 37: 114–116.

On présente une version corrigée mathématiquement d'une méthode déjà publiée d'analyse des résultats d'expériences de double étiquetage. Des données sur les retours d'étiquettes de homard servent à illustrer le protocole analytique.

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IN correspondence with Jay S. Krouse (State of Maine, Dep. Mar. Res.) regarding his efforts in analyzing data from double-tagging experiments on American lobsters using methods described by Gulland (1963), I was able to demonstrate errors in Gulland's notation[1] that had been responsible for Krouse's initial, erroneous results.

At a recent U.S.–Canadian workshop on lobster biology and management it became apparent that other workers had also encountered difficulties in applying Gulland's method to double-tagging experiments.

This note is in response to an apparent need for supplementing the current literature dealing with the estimation of the rate of tag loss by the double-tagging method.

The mathematical argument — From Gulland's (1963) notation where fish are marked with two tags which may be of different types having different and independent probabilities of loss,

$_AP_t$ = probability of loss of tag A over time t
$_BP_t$ = probability of loss of tag B over time t
$(1 - {_AP_t})$ = probability of retention of tag A over time t
$(1 - {_BP_t})$ = probability of retention of tag B over time t

Then,

$_1N_A = {_BP_t}(1 - {_AP_t})$
= probability of retention of tag A and loss of tag B over time t
$_1N_B = {_AP_t}(1 - {_BP_t})$
= probability of retention of tag B and loss of tag A over time t
$_2N = (1 - {_AP_t})(1 - {_BP_t})$
= probability of retention of both tags A and B over time t
$_0N = ({_AP_t})({_BP_t})$
= probability of loss of both tags over time t

The 1-tag: 2-tag ratios are,

$$(1) \quad \frac{_1N_A}{_2N} = \frac{_BP_t(1 - {_AP_t})}{(1 - {_AP_t})(1 - {_BP_t})} = \frac{_BP_t}{(1 - {_BP_t})}$$

$$(2) \quad \frac{_1N_B}{_2N} = \frac{_AP_t(1 - {_BP_t})}{(1 - {_AP_t})(1 - {_BP_t})} = \frac{_AP_t}{(1 - {_AP_t})}$$

Gulland (1963) incorrectly gave for the right-hand members of expressions (1) and (2),

$$\frac{_BP_t}{(1 - {_AP_t})} \text{ and } \frac{_AP_t}{(1 - {_BP_t})}, \text{ respectively.}$$

It is clear that simultaneous with the loss of tag A, tag B may be either retained or lost as well. The latter case, though undetectable, is still a component of the total probability function describing the loss of tag A. However, because,

$$_AP_t = {_AP_t}(1 - {_BP_t}) + ({_AP_t})({_BP_t})$$

it is unnecessary to consider explicitly the function, $_0N$.

From tag return data, the functions necessary for evaluating the 1:2 tag ratios are defined by setting,

$_1N_A$ = number of returns with tag A only
$_1N_B$ = number of returns with tag B only
$_2N$ = number of returns with both tags A and B

In the case where rate of tag loss is constant, then linear regressions against time of the ratios $_1N_A/_2N$ and $_1N_B/_2N$, computed over appropriate time intervals, allow estimation of their annual values and thus annual probabilities of tag loss from expressions (1) and (2).

Application to tag return data — Data from Krouse's (1977) lobster tagging study at Kennebunkport, Maine were made available for this paper. Examination of

TABLE 1. Representative calculations for determination of the annual probability of tag loss from the results of a double-tagging experiment. Data are from Krouse (1977). Weighted mean time at liberty is given in brackets.

t (weeks)	$_1N_A$[a]	$_2N$[c]	$_1N_A/_2N$
0– 4 (3.252)	6	136	0.044
5– 8 (6.347)	18	184	0.098
9–12 (10.440)	13	64	0.203
13–16 (14.144)	22	101	0.218
17–20 (18.292)	9	29	0.310
21–24 (22.353)	3	9	0.333

$_1N_A/_2N = 0.008 + 0.016t \quad (r^2 = 0.965)$
let $t = 52$ wk
Then,

$$_1N_A/_2N = 0.814 = \frac{_BP}{(1 - {_BP})}$$

$_BP = 0.449$[e]

t (weeks)	$_1N_B$[b]	$_2N$[c]	$_1N_B/_2N$
0– 6 (4.161)	30	236	0.127
7–12 (8.847)	24	148	0.162
13–18 (14.757)	31	116	0.267
19–24 (20.912)	7	23	0.304

$_1N_B/_2N = 0.077 + 0.011t \quad (r^2 = 0.960)$
let $t = 52$ wk
Then,

$$_1N_B/_2N = 0.667 = \frac{_AP}{(1 - {_AP})}$$

$_AP = 0.400$[d]

[a] $_1N_A$ = number of returns with sphyrion tag only.
[b] $_1N_B$ = number of returns with cinch-up tag only.
[c] $_2N$ = number of returns with both types of tags.
[d] $_AP$ = annual probability of loss of sphyrion tag.
[e] $_BP$ = annual probability of loss of cinch-up tag.

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[1] Mr. Gulland notes that the errors were first pointed out to him in correspondence (1968) with Dr J. S. Hynd, CSIRO, Division of Fisheries and Oceanography, P.O. Box 21, Cronulla, Sydney NSW 2230, Australia.

the original data suggested that the rate of loss of both types of tags, the sphyrion anchor tag (Scarratt and Elson 1965; Cooper 1970), and the Floy cinch-up tag, was probably a linear function of time subsequent to release. Accordingly, linear regressions of the 1:2 ratios on mean time in weeks at liberty were run after grouping data by intervals of one to six weeks. By this procedure it was determined that the best fit to a linear function was achieved with 4-wk intervals in the case of the ${}_1N_A/{}_2N$ ratio and 6-wk intervals for the ${}_1N_B/{}_2N$ ratio. As Gulland (1963) has implied, there is no constraint to treat the two sets of data relating to loss of each type of tag in an identical manner with respect to the choice of an appropriate system for grouping the data.

Results — Fishing mortality rates in the lobster fishery of the Kennebunkport area on the coast of Maine are apparently very high. Krouse (1977) estimated $F = 2.99$. The result was a paucity of later returns from Krouse's tagging activity. Thus, in all cases, this analysis was restricted to the first 25 wk following release of the tagged animals.

The analysis of grouped data from Krouse (1977) appears in Table 1. Linear regressions of the respective 1:2 ratios, when extrapolated to a period of 1 yr, indicated that the ratio of lobsters carrying the sphyrion tag alone to those carrying both tags was 0.814. From expression (1), this indicated that the annual probability of loss of the cinch-up tag was 0.449. Similarily, the ratio of cinch-up tag:double-tagged lobsters was estimated to be 0.667 indicating an annual probability of loss of the sphyrion tag of 0.400. Finally, it may be noted that the annual probability of loss of both tags is the product of the annual probabilities of loss of each tag, which in this case was 0.180.

Acknowledgments — I am indebted to Jay Krouse for initially alerting me to the existence of the problem and for kindly allowing the use of his data as an example for this paper.

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Concentrations of Leucine Aminonaphthylamidase (LAN) and Soluble Protein in Tissues of Rainbow Trout, *Salmo gairdneri*

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BOUCK, G. R. 1980. Concentrations of leucine aminonaphthylamidase (LAN) and soluble protein in tissues of rainbow trout, *Salmo gairdneri*. Can. J. Fish. Aquat. Sci. 37: 116–120.

The levels of soluble protein (Biuret-reactive) and levels of leucine aminonaphthylamidase (LAN, 3.4.1.1) were determined quantitatively in extracts of 10 organs from rainbow trout (*Salmo gairdneri*). Soluble protein had a very discrete distribution and averaged 5.2 times more concentrated in liver than in blood plasma (3.5 g/100 mL). LAN was present in the extract of every tissue except saline-washed brain. LAN activity was highest in hindgut, 36 more times more concentrated than in the plasma of healthy fish. Wasting disorders such as caused by stress, would likely increase the level of necrosis which in turn would increase the amount of LAN in plasma. I propose that a "tissue equivalent" unit of LAN to provide a means of relating increased LAN in plasma to an amount of liver destruction in vitro that would render a similar amount of LAN.

Key words: plasma enzymes, stress, plasma protein, rainbow trout, leucine aminonaphthylamidase, fish physiology

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BOUCK, G. R. 1980. Concentrations of leucine aminonaphthylamidase (LAN) and soluble protein in tissues of rainbow trout, *Salmo gairdneri*. Can. J. Fish. Aquat. Sci. 37: 116–120.

Nous avons déterminé quantitativement, sur des extraits de dix organes de truite arc-en-ciel (*Salmo gairdneri*), les niveaux de protéines solubles (réactives au Biuret) et ceux de la leucine aminonaphthylamidase (LAN, 3.4.1.1). Les protéines solubles ont une distribution très disjointes et sont en moyenne 5,2 fois plus concentrées dans le foie que dans le plasma sanguin (3,5 g/100 mL). La LAN est présente dans l'extrait de chaque tissu, sauf le cerveau lavé à une saline. L'activité de la LAN est maximale dans l'intestin inférieur, 36 fois plus concentrée que dans le plasma de poissons sains. Des troubles atrophiants, tels que ceux causés par le stress, élévéraient probablement le niveau de nécrose, ce qui, à son tour, augmenterait la quantité de LAN dans le plasma. Je propose une unité en «équivalent tissu» de LAN qui permettrait de relier une augmentation de LAN dans le plasma à un degré de destruction du foie in vitro qui donnerait une quantité semblable de LAN.

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BASED on reports that stress causes wasting disorders which in turn elevate leucine aminonaphthylamidase (LAN 3.4.1.1) in plasma (PLAN) of vertebrate animals (Hess 1963; Simon 1970), I believed that LAN might be useful in assessing fish health. The histochemical distribution of LAN has already been reported (Bouck 1979). The use of PLAN in fish health, however, is hindered by the lack of data to indicate its significance. Specifically there is a lack of clinical data associating PLAN levels with toxicity and other health risks both for individuals and populations. Such data require rather long and extensive efforts which are not likely to occur in fisheries research in the near future. As an alternative approach one can relate increases of PLAN in vivo to an amount of tissue destruction in vitro which would yield an equivalent amount of LAN. Prerequisites to this goal required quantitative estimates of LAN and soluble protein in various tissues of rainbow trout; the goal of this research was to provide these data.

LAN is a proteolytic enzyme that is found mainly in the lysosomes of cells (Kaulen et al. 1970) and is activated by and assists in the autolytic process of dying or dead cells. Hence, the physiological basis for LAN in plasma is the continuous process of cell death. Guyton (1961) estimates that a typical human is composed of about 100 trillion cells, of which about 1% are replaced daily. When a cell dies, a portion of its enzyme "debris" passes thru the interstitial spaces and lymphatic system to become a transitory constituent of blood. During periods of increased cell death, increased amounts of cellular enzymes pass into the blood and accordingly, the activity of LAN rises in the plasma or serum (Hess 1963; Bouck et al. 1975). Other factors can cause elevated levels of enzymes including corticosteroids (Goldstein et al. 1962), but again, these are usually related to stressful conditions.

PLAN has several potential advantages as an indicator of stress in fish. Its maximal activity occurs considerably above room temperature, which in turn can preclude the usual need for refrigeration during its assay (Bouck et al. 1975). The stress from capture of fish does not significantly alter levels of PLAN (Bouck et al. 1978) provided the blood samples are collected within a few minutes after initiation of capture struggles. In theory LAN is located exclusively in lysosomes (DeDuve 1959) and therefore its appearance in blood is associated with cellular destruction.

Materials and methods — Rainbow trout (*Salmo gairdneri*) from Roaring River Hatchery, Oregon, were reared to subadult stage on Oregon Moist Diet II and these ranged from 13 to 17 cm total length. Each fish was killed by cutting the cervical vertebrae. The desired tissue was excised as rapidly as possible, weighed, diluted appropriately with 0.9% NaCl and then disrupted in an ice-cooled glass mortar with a Teflon pestle. The gut lumens were washed in a stream of 0.9% NaCl to remove possible contaminants, and rolled on filter paper to remove excess moisture before being weighed. This procedure was also used for washing brain where so indicated. Collateral studies demonstrated that sonication of the slurry produced slightly higher levels of LAN in the subsequent extract in some cases but also increased the risk of heat denaturation; for these reasons sonication was omitted. The slurry was centrifuged at 45 000 × *g* and 0°C for 90 min. The resulting supernate was clear, but slightly colored in some tissues. Total amounts of supernate and sediment were used to estimate the total amount of LAN both in the extract and in the extracted tissue.

Protein concentration was determined by a modification of Weichselbaum's (1946) method as follows: 0.05 mL of sample was added to 2.00 mL of Weichselbaum Biuret reagent. This was reacted at room temperature for at least 30 min after which the color was stable for at least 2 d. Absorbancy at 510 nm was determined and converted to equivalent grams of bovine serum albumin per 100 mL by an experimentally determined regression equation.

LAN activity was determined by a modification (Bouck et al. 1975) of the basic method of Goldbarg and Rutenburg (1958). Substrate was prepared by mixing equal volumes of 0.4 mg *L*-leucyl-β-naphthylamide per millilitre of water, with 0.2 mol/L tris (hydroxymethyl)-aminomethane at pH 8.0. To 0.05 mL of sample was added 1 mL of substrate and the mixture was incubated 1 h at 20°C, whereupon the enzyme was denatured by adding 1 mL of 40% trichloracetic acid. The sample was then centrifuged lightly to precipitate the protein. Then 1 mL of the deproteinized

TABLE 1. Summary of dilutions, concentrations of soluble protein, and activities of leucine aminonaphthylamidase (LAN) in tissues of rainbow trout (*Salmo gairdneri*). Mean ± SE; $n = 10$ for all tissues except hindgut where $n = 7$.

Tissue	Required dilution[a]	Extracted soluble protein (g/100 g of tissue)	LAN activity per gram of soluble protein[b]	LAN activity per gram of tissue[b]
Blood plasma	0	3.52±0.16	20.20±1.19	0.67±0.03
Brain (unwashed)	1:4	1.98±0.05	154.76±17.14	2.73±0.76
Brain (washed)	1:4	1.73±0.03	0.00	0.00
Foregut	1:4	6.76±0.08	55.92±4.47	1.49±0.13
Gill	1:9	3.61±0.03	79.06±9.22	2.70±0.26
Heart	1:9	2.89±0.02	183.14±13.50	5.27±0.46
Hindgut	1:49	5.28±0.35	449.09±91.48	24.50±5.50
Kidney	1:9	5.31±0.02	69.85±3.64	3.70±0.20
Liver	1:9	18.16±0.23	54.37±6.98	8.51±0.34
Midgut	1:9	8.37±0.08	355.64±114.70	24.43±1.58
Skeletal muscle	1:4	9.26±0.07	50.95±3.34	2.28±0.09
Spleen	1:9	6.70±0.06	67.01±5.94	4.27±0.28

[a] Ratio of 1 g of tissue to millilitres of 0.9% NaCl.

[b] One unit of LAN activity represents the hydrolysis of 1 mmol of 1-leucyl-β-naphthylamide per hour at 20°C.

sample was mixed with 1 mL of 0.1% sodium nitrite and allowed to react for 3 min. The nitrite was decomposed by adding 1 mL of 0.5% ammonium sulfamate and allowing it to react for 2 min, before 2.0 mL of 0.05% *N*-(1-naphthyl)-ethylenediamine:HCl was added and reacted for 20 min. The absorbancy of the naphthylamide residue was measured at 585 nm after zeroing the spectrophotometer against a reagent blank, and converted to micromoles of naphthylamide per sample. Each unit of LAN activity was equivalent to the production of 1 μmol of naphthylamide per hour at 20°C. This incubation temperature was selected because it is compatible with more labile enzymes such as lactate dehydrogenase. Tissues were sampled and tested individually from at least 10 fish.

Results and discussion — Most of the tissue extracts required dilution to retain the LAN activity within zero-order kinetic limits, i.e. less than 0.09 μmol β-naphthylamine produced in all per test. The dilutions that proved acceptable are listed in Table 1, and ranged from 1:49 for hindgut to no dilution for washed brain, but a 5- or 10-fold dilution was adequate for other tissues.

Soluble protein in tissues — The extracted soluble protein for each tissue is listed in Table 1. As a reference point, blood plasma protein averaged about 3.5 g/100 mL, which is typical of freshwater adapted, sexually immature rainbow trout. Brain and heart had less soluble protein that any other tissue, while that in gill was about equal to blood plasma. Conversely, most of the tissues had substantially higher concentrations of soluble protein, and liver had 5 times the concentration of protein in plasma.

A concentration gradient clearly exists for soluble proteins (Table 1) and favors their net movement from the cell to the plasma. The healthy cell membrane retains proteins until it becomes moribund or necrotic; otherwise the protein concentrations would become equal in cells and in plasma. This illustrates the general proposition that cellular metabolites including enzymes (proteins) can enter the plasma as a result of cell damage, and therefore may serve as a diagnostic indication of stress particularly from toxicity.

The dynamic interaction between cellular proteins and plasma proteins is not clear and deserves greater attention. Probably all of the soluble proteins in a fish can be viewed as potential, albeit transitory components of the blood plasma. Furthermore, it is clear that the pool of soluble protein in some tissues is relatively large compared to that in the plasma. From this, one might predict that stress in fish could cause a qualitatively significant loss of protein from cells to blood, thus causing a hyperproteinemia. This hypothesis is supported by my observations (unpublished) that plasma protein concentrations in spawning rainbow trout and coho salmon (*Oncorhynchus kisutch*) were significantly higher, typically between 5–6 g/100 mL, than in subadult life stages. Conversely, plasma protein concentrations among subadult rainbow trout on Oregon Moist Pellets (Diet II) are relatively stable until they are stressed, when they typically become hypoproteinemic but with increased plasma enzyme activities. Thus the stress–hyperproteinemia hypothesis may hold true for certain proteins but does not always apply to total plasma protein. Such a broad range of plasma protein concentrations argues, that unlike humans, rainbow trout probably do not have a rapidly responding active homeostatic mechanism to control closely protein level in the plasma.

LAN in tissues — The biochemical method of assaying LAN proved to be considerably more sensitive than the histochemical method. Bouck's (1979) histochemical study of LAN was unable to detect low levels of LAN activity and hence negative indications for LAN were reported for spleen, foregut, skeletal muscle, and blood cells. Based on the biochemical assay, LAN is present in all of the tissues (except possible brain and blood cells) (Table 1). From these data, it is obvious that LAN activity varies widely between different tissues and therefore has a very heterogeneous distribution within a fish, within its tissues, and within its cells.

Brain (washed) had virtually no LAN activity, but heart was moderately rich in LAN. Within the gastrointestinal tract, foregut (stomach) had little LAN activity, but midgut and hindgut had the highest LAN levels in the body. LAN was about 15 times more concentrated in the midgut and hindgut than in the stomach. This distribution indicates a considerable difference both in digestive capacities based on the hydrolysis of leucine moieties and in physiological function between these locations. The amount of LAN activity in cerebrospinal fluid was not determined. However, saline-washed brain contained no detectable LAN activity, while unwashed brain had significant amounts of LAN activity, especially when compared per gram of soluble protein. This difference seems due to the removal of cerebrospinal fluid and possible meningeal tissue from the excised brain. An alternative hypothesis is that some aspect of the washing procedures inhibited the activity of LAN in the brain but not in the gut, and this seems untenable. Thus it appears that cerebrospinal fluid may be well endowed with the proteolytic enzyme LAN, possibly above the level normally found in blood plasma, but its significance is unknown.

The absence of LAN from brain compared to the high levels of LAN in heart seem paradoxical. One can speculate that brain might be an unfavorable location for LAN, because normal cell death might then release LAN or other proteolytic enzymes which in turn could go on to damage other neurons. Conversely, heart might benefit from having LAN because it could assist the removal of dead cells that might otherwise impede the transmission of cardiac excitation.

Relationship of tissue LAN to plasma LAN — It is apparent that a significant concentration gradient exists between the LAN in tissues and in plasma (Table 1). Damage to any tissue but brain would tend to favor equilibrium which would increase the LAN in blood plasma (PLAN). However, an equal weight of necrosis or other damage between different tissues would not necessarily produce equal elevations in PLAN. This disparity stems both from the different concentrations of LAN in different tissues and from the different locations of LAN-rich cells within tissues. For example, on the basis of tissue LAN concentration, liver damage could produce nearly four times the amount of PLAN as would a similar amount of damage in skeletal muscle. On the other hand, Bouck (1979) reported that LAN in the midgut, ceca, and hindgut was located mainly in the mucosal epithelium; their damage might cause LAN liberation more into the lumen of the gut rather than into the blood. Likewise Bouck (1979) also reported that in kidney, LAN is present primarily in the epithelium of certain portions of the tubules, hence liberated LAN could pass either into the urine or into the blood.

The elimination of enzymes from blood has not been studied in fish but avenues for their elimination exist. Enzyme elimination may occur by pinocytosis among various cells, by glomerular filtration losses to urine, by enzyme breakdown, by inhibition by biochemicals in the plasma, and possibly by other means. Also, the dynamics of enzyme elimination probably differ between healthy and nonhealthy fish.

Tissue equivalent of LAN levels — The diagnostic use of LAN and other plasma enzymes is impeded by a lack of experimentally derived statistical ranges which identify sick or healthy fish. Until such diagnostic aids are available, the biological significance of PLAN might be placed in a more useful perspective if its enzyme activity were expressed as that weight of a tissue which, if destroyed, would yield an equivalent amount of LAN in vitro. Such a "Tissue Unit" could supplement the standard international unit of enzyme activity (International Chemistry Union), not replace it. Liver is proposed as a standard for these purposes, which in this case yielded an average of 8.5 international units (IU) of LAN per gram of tissue. Liver seems appropriate for this purpose because many stressor agents cause liver damage.

The use of a proposed tissue unit requires the estimation of total plasma volume based on an assumed total blood volume equal to 6% of body weight (Smith 1966) and hematocrit level:

$$\text{(a) Total plasma (mL)} = (0.06 \times \text{body wt.}) \times (100\% - \text{hematocrit } \%);$$

$$\text{(b) Total plasma PLAN} = \frac{\text{Units PLAN}}{\text{mL plasma}} \times \text{mL total plasma};$$

$$\text{(c) Tissue Equivalent Units} = \frac{\text{Total PLAN}}{8.5 \text{ IU/g liver}}$$

An example calculation will illustrate this: (1) *control fish* weighed 100 g, had hematocrits of 30%, and PLAN activity at 0.67 IU/mL of plasma; (2) experimental fish weigh 95 g but had hematocrits of 25% and 6.7 IU of PLAN/mL of plasma. Therefore the tissue (liver) equivalent units of PLAN would be 0.33 g of liver in the controls and 3.37 g of liver in the experimental fish. Thus the rise in PLAN is mathematically equivalent to the in vitro destruction of about 3 more grams of liver per fish in the experimental group. This comparison is not intended to convey a strict quantitative relationship between levels of PLAN and liver necrosis in vivo. However, it may help to provide a method for comparing plasma enzyme data from fish with varying treatments and relates to how the enzyme enters the blood.

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Interspecific Predation of Common Strait of Georgia Planktonic Coelenterates: Laboratory Evidence

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ARAI, M. N., AND J. R. JACOBS. 1980. Interspecific predation of common Strait of Georgia planktonic coelenterates: laboratory evidence. Can. J. Fish. Aquat. Sci. 37: 120–123.

Among the common pelagic coelenterates of Departure Bay, B.C., *Stomotoca atra*, *Eutonina indicans*, *Aequorea victoria*, and *Aurelia aurita* show predation on other species under laboratory conditions. Selectivity is demonstrated in the diets of each of these predators.

Key words: Stomotoca atra, Eutonina indicans, Aequorea victoria, medusae, feeding, *Aurelia aurita*

ARAI, M. N., AND J. R. JACOBS. 1980. Interspecific predation of common Strait of Georgia planktonic coelenterates: laboratory evidence. Can. J. Fish. Aquat. Sci. 37: 120–123.

Parmi les coelentérés pélagiques communs de la baie Departure, C.-B., *Stomotoca atra*, *Eutonina indicans*, *Aequorea victoria* et *Aurelia aurita* sont prédateurs d'autres espèces dans des conditions de laboratoire. Chacun de ces prédateurs fait preuve de sélectivité de leurs proies.

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MEDUSAE and ctenophores have been recognized as important tertiary carnivores in the food web of marine planktonic communities (Petipa et al. 1970). Huntley and Hobson (1978) showed that predation by medusae such as *Phialidium gregarium* can reduce the herbivor-

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ous zooplankton to such an extent that grazing pressure on the phytoplankton is significantly affected. Medusae are also both predators on, and competitors with fish. Little is known about interspecific predation by medusae however. Whereas interspecific predation has been studied in ctenophora and predator–prey species pairs characterized (Greve 1970, 1971, 1972), data on medusae predation on other coelenterates have been limited to casual references in general feeding studies or natural history papers. Moreover, little of even these observations is pertinent to the common species of British Columbia waters. The present study was therefore undertaken to identify local medusa species showing predation on other coelenterates and to examine the degree of specificity shown in prey selected.

The general feeding studies mentioned above have been carried out either by analysis of stomach contents or by detailed observation of feeding of a few animals in aquaria. Both methods proved unsatisfactory for the present study. Investigations of stomach contents (e.g. McCormick 1969; Zelickman et al. 1969; Zelickman 1976) usually show only small numbers of medusae with identifiable prey and proportionately increase the numbers of prey with hard exoskeletons. It is also not possible to demonstrate clearly lack of predation on particular species when contacts in the plankton must be assumed. Intensive observations of a few specimens in the laboratory (e.g. Lebour 1922, 1923; Plotnikova 1961; Sveshnikov 1963; Fraser 1969) may yield good detailed data on feeding behavior but are unsuitable for a general survey. Thus for the purposes of this study it was decided to perform laboratory experiments in which a small group of possible predators was placed with an equal number of possible prey and the number of prey eaten noted after 24 h. This allowed a large number of combinations to be examined for predation in a manageable period.

Materials and methods — Specimens were dipped from the sea using glass containers. *Sarsia princeps* (Haeckel 1879), *S. tubulosa* (M. Sars 1835), *Bougainvillia multitentaculata* Foerster 1923, *Stomotoca atra* Agassiz 1862, an undescribed species of *Leuckartiara*, *Melicertum octocostatum* (M. Sars 1835), *Obelia*, *Phialidium gregarium* (Agassiz 1862), *Eutonina indicans* (Romanes 1876), *Aequorea victoria* (Murbach and Shearer 1902), *Proboscidactyla flavicirrata* Brandt 1835, *Aurelia aurita* (Linnaeus 1758), and *Pleurobrachia pileus* (O. F. Muller 1776) var *bachei* Agassiz 1860 were obtained from Departure Bay or Ladysmith Harbour. *Mitrocoma cellularia* (Agassiz 1865) and *Eperetmus typus* Bigelow 1915 are rare in these bays and were obtained from Cowichan Bay and Sooke Harbour, respectively. All specimens were transferred to Departure Bay water and maintained at least 16 h prior to testing at the temperature (13°C) and salinity of the water used in experiments. Most were used within 3 d but active and well-fed predators were used in some experiments up to 6 d after capture.

Experiments were conducted by placing five possible predator specimens and five possible prey specimens in fresh sea water in 3.6 L glass jars maintained at 13°C. The number of prey eaten after 24 h were noted. Normally only duplicate experiments were run; however, in 12 combinations where the results were considered doubtful, usually due to poor condition of prey when attacked but not eaten, the experiments were repeated until consistent results were achieved. The number of combinations tested for each species depended on its availability in the plankton during the experimental period May to August.

Results — Table 1 summarizes predation by the four main species for which medusan prey was indentified; *Stomotoca atra*, *Eutonina indicans*, *Aequorea victoria*, and *Aurelia aurita*.

Stomotoca atra is a pandeid anthomedusan. Hyman (1940) noted predation on *Phialidium*. It was found to eat the eight hydrozoan species tested as well as the scyphozoan *Aurelia aurita*. It was the only predator identified for the two limnomedusae *Eperetmus typus* and *Proboscidactyla flavicirrata*. However, it showed no predation on the common ctenophore *Pleurobrachia pileus*.

Eutonina indicans, a leptomedusan, was shown by Greve (1972) to eat *Pleurobrachia*. This was verified. It was also found to eat the scyphozoan *Aurelia aurita* but of 11 species of hydrozoa tested showed significant predation only on the two species of *Sarsia*.

Aequorea victoria, a leptomedusan, has not been previously examined for coelenterate predation. It ate *Sarsia*, *Aurelia*, *Pleurobrachia*, and the other leptomedusae tested but not the two limnomedusae.

Aurelia aurita, a scyphozoan was most extensively examined by previous investigators. Ephyrae eat *Obelia* and *Rathkea octopunctata* (Husing 1956, Loginova and Perzova 1967). The former was verified. Two centimeter diameter *A. aurita* ate *Laodicea* (Fraser 1969). Twenty to 25 millimeter *A. aurita* ate *Rathkea octopunctata* and *Phialidium* sp. (Lebour 1923). The latter was also verified. Greve (1972) stated that *Aurelia* adults do not eat *Pleurobrachia pileus*. Adults are largely microphagous, feeding by ciliary currents (Southward 1955). The present study shows, however, that intermediate size *Aurelia* will eat *Pleurobrachia* and also *Sarsia*.

The last three species were tested in more that one size-class. In each case greater amounts of predation by larger sizes of predator were found. When larger specimens were tested against smaller specimens of the same species no predation was noted.

Several other species were also investigated for possible predation on other coelenterates. The most extensively available for testing were *Sarsia tubulosa*, *Phialidium gregarium*, and *Proboscidactyla flavicirrata*. No predation was demonstrated for these three species.

Sarsia tubulosa (as *Sarsia mirabilis*) was observed by Agassiz (1862) swallowing "large numbers of small medusae, and especially other species of hydroid medusae and the young of *Aurelia flavidula*." Forbes (1848) stated that it ate *Rathkea octopunctata* and Sveshnikov (1963) that it ate *Obelia geniculata*. On the other hand Plotnikova (1961) found no predation

TABLE 1. Predation by four species of coelenterates on other coelenterates, number eaten per 10 prey tested. P represents experiments in which the predator was eaten by the putative prey, blanks represent untested combinations.

	Predators								
	Stomotoca atra	*Eutonina indicans*		*Aequorea victoria*		*Aurelia aurita*			
Prey species	>10 mm	10–15 mm	>15 mm	8–20 mm	20–40 mm	ephyrae	<8 mm	8–18 mm	18–28 mm
Anthomedusae									
Sarsia princeps adults		0	4	4		0			
Sarsia tubulosa adults	8	8	7	3	10	0		2	4
Bougainvillia multitentaculata	6		0						
Leuckartiara sp. adults		0			0	P		0	
Leptomedusae									
Melicertum octocostatum — 4–8 mm		0							
Mitrocoma cellularia — 20–40 mm	9		0						
Obelia				10		4			
Phialidium gregarium — 4–8 mm	10	0	0				0	0	
— >8 mm	10	0	1	5	7	0	0	0	3
Eutonina indicans — 10–15 mm	10	0	0	6	10	P	0	0	1
— >15 mm	6	0	0	7	10	P	P	0	
Aequorea victoria — 5–8 mm		0			0			0	0
— 8–20 mm	10	P	P	0		P	P	P	
Limnomedusae									
Eperetmus typus — 9–16 mm	6		0	0	0			0	
Proboscidactyla flavicirrata — 4–7 mm	10	0	0	0	0	0	0	0	0
Scyphomedusae									
Aurelia aurita — ephyrae	6	1	10	4	9	0		0	0
— <8 mm	6	0	9	1	4		0		
— 8–18 mm		0	0	1	5	0		0	
Ctenophora									
Pleurobachia pileus — 2–4 mm		1						6	
— 5–9 mm	0	3	4	6	10	0	0	0	1
— >9 mm	0	0	9	4	10	0	0	0	0

on small ctenophores, *Rathkea* or *Obelia*. In the present study no predation by adult *S. tubulosa* was found on *Phialidium* (even in the 4–8 mm size-class), *Proboscidactyla flavicirrata* (4–7 mm), *Aurelia aurita* (even ephyrae), or *Pleurobrachia pileus* (even 2–4 mm). This lack of predation was not due to the experimental conditions as copepods and fish larvae were eaten under the same conditions.

Phialidium gregarium >8 mm diameter did not show any predation on *Sarsia princeps* adults, *S. tubulosa* adults, *Proboscidactyla flavicirrata* 4–7 mm, *Aurelia aurita* ephyrae, or *Pleurobrachia pileus* 2–4 mm. There was also no predation on smaller (4–8 mm) *P. gregarium*. *Proboscidactyla flavicirrata* (4–7 mm diameter) showed no predation on *Sarsia princeps* (adults), *S. tubulosa* (adults), *Melicertum octocostatum* (4–8 mm), *Phialidium gregarium* (4–8 mm), *Aurelia ephyrae*, or *Pleurobrachia pileus* (2–4 mm).

The testing of other species was limited by availability in the collecting areas. An undescribed species of *Leuckartiara* is occasionally present in Departure Bay which reaches a maximum bell height of 5 mm plus a dome of up to 5 mm. It showed predation (3/10) on Aurelia ephyrae but not larger *Aurelia* or *Proboscidactyla flavicirrata* 4–7 mm. *Obelia* were not found to eat other *Obelia* as suggested by Lebour (1922, 1923). *Eperetmus typus* (9–16 mm diameter) showed no predation on *Sarsia tubulosa, Phialidium gregarium* >8 mm, *Proboscidactyla flavicirrata* (4–7 mm), or *Pleurobrachia pileus* >9 mm.

Discussion — Four of the common planktonic coelenterates of Departure Bay have been shown to eat other coelenterates under laboratory conditions. Figure 1 illustrates a tentative coelenterate food web derived from this information. Field work is now in progress to establish the exact sequence of appearance of the various species and whether prey of appropriate sizes will be present in the plankton in significant numbers at the same time as potential predators. Preliminary results indicate that one other species is common in the bay in March and April, i.e. before the laboratory work was begun. This species is *Rathkea octopunctata* which has been stated by Lebour (1923) to eat *Phialidium* and by *Plotnikova* (1961) to eat *Bolinopsis infundibulum*. Although it is a very small species (up to 4 mm high) it may show predation on the young stages of other medusae which are common in the bay in early spring.

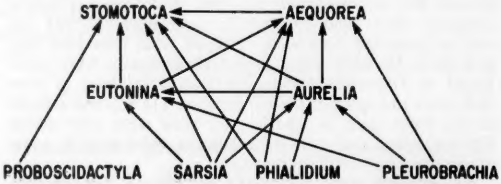

FIG. 1. Food web of the common pelagic coelenterates of Departure Bay, British Columbia.

The above data clearly demonstrate selectivity in the diets of the four common species that show predation on other coelenterates. However, no predator was dependent on a single prey species. It is difficult to evaluate the degree of competition involved. Not only do the four species vary in period of maximum abundance in the bay but all four species will accept noncoelenterate prey. This study will be extended to investigate predation on other possible prey including fish larvae.

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Leaf Litter Processing in a Regulated Rocky Mountain Stream

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SHORT, R. A., AND J. V. WARD. 1980. Leaf litter processing in a regulated Rocky Mountain stream. Can. J. Fish. Aquat. Sci. 37:123–127.

Processing of alder (*Alnus tenuifolia*) was investigated during autumn and winter to determine the influence of stream regulation on leaf litter processing. Study sites were the Colorado River below Granby Dam and the Fraser River, an unregulated tributary. Alder leaves (5-g units) were attached to bricks and placed in riffles. Leaching controls were retrieved after 48 h; thereafter five replicates were collected from each site after 17, 38, 52, and 66 d. There were significant differences ($P < 0.05$) in processing rates between sites. The loss rate coefficient (k) was much higher ($k = 0.0462$) for leaves incubated in the regulated section

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of the Colorado River than for those in the unregulated tributary (k = 0.0235). The hypothesis that reductions in macroinvertebrate shredders would decrease processing rates of leaf litter in regulated streams was not supported by the results. The "winter warm" thermal regime below the reservoir seems to compensate for the virtual absence of shredder species apparently by enhanced microbial processing.

Key words: Colorado River, leaf litter, macroinvertebrates, Rocky Mountains, stream regulation, temperature

SHORT, R. A., AND J. V. WARD. 1980. Leaf litter processing in a regulated Rocky Mountain stream. Can. J. Fish. Aquat. Sci. 37: 123–127

Dans le but de déterminer l'influence du contrôle d'un cours d'eau sur la transformation de la litière de feuilles dans un cours d'eau des montagnes Rocheuses, nous avons étudié la transformation de l'aulne (*Alnus tenuifolia*) en automne et en hiver. Les recherches ont été effectuées sur le fleuve Colorado, en aval du barrage Granby et sur la rivière Fraser, un tributaire non contrôlé. Des feuilles d'aulne (unités de 5 g) furent attachées à des briques et placées dans des «maigres» le 29 septembre. Des témoins de lessivage furent enlevés après 48 h; par la suite, 5 reproductions furent recueillies à chaque site après 17, 38, 52 et 66 jours. Il y a des différences significatives ($P < 0,05$) de taux de transformation entre les sites. Le coefficient de taux de perte (k) est beaucoup plus élevé (k = 0,0462) pour des feuilles incubées dans la section contrôlée du fleuve Colorado que celles placées dans le tributaire non contrôlé (k = 0,0235). Les résultats de cette étude n'appuient donc pas l'hypothèse que la diminution des macroinvertébrés déchiqueteurs ralentit la transformation de la litière végétale dans des cours d'eau contrôlés. Le régime thermique de «chaleur hivernale» en aval du réservoir semble compenser l'absence virtuelle d'espèces déchiqueteuses par une transformation microbienne plus active.

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DETERMINATIONS of leaf litter processing rates have generated a great deal of information concerning stream ecosystem structure and function (e.g. Petersen and Cummins 1974; Sedell et al. 1975; Benfield et al. 1977) and have provided an experimental means to test various hypotheses (Reice 1974, 1977). The leaf pack method has also been used as a bioassay to determine the effects of man's activities on streams (Triska and Sedell 1976; Gelroth and Marzolf 1978). One significant anthropogenic impact has been the construction of numerous reservoirs on previously free-flowing streams. Large dams may greatly modify the physicochemical conditions of downstream reaches with resultant changes in the diversity, density, and composition of the macroinvertebrate fauna (Ward 1976a; Ward and Stanford 1979). Since there is a selective elimination of certain taxonomic and functional groups (Ward and Short 1978), it was hypothesized that leaf litter processing would be altered by stream regulation. The leaf pack method was utilized to determine the influence of stream regulation by dams on leaf litter processing rate.

Materials and methods — Study area — Study sites were on the Colorado River below Lake Granby and on the Fraser River, a major tributary unregulated by dams. Lake Granby is a large storage reservoir located 10 km northeast of Granby in the Rocky Mountains of northern Colorado. The dam is 91 m high and impounds 666 × 10^6 m^3 of water. The confluence of the Fraser and Colorado rivers is 12 km below Granby Dam. A site on the Fraser River was selected immediately upstream from Granby.

Study locations were at comparable elevations (2460 and 2420 m a.s.l.) and exhibited generally similar conditions. Woody riparian vegetation consisted predominantly of willows (*Salix* spp.) and alder (*Alnus tenuifolia*) and the stream bottom was predominantly rubble in both study sections. During the study period, discharge averaged 0.54 m^3/s in the Colorado River and 0.53 m^3/s in the Fraser River. Total dissolved solids (35.7 mg/L; 65.4 mg/L) and methyl orange alkalinity (11.0 mg/L; 22.5 mg/L) values were somewhat higher in the Fraser River. Nitrogen–nitrate (53 $\mu g/L$; 43 $\mu g/L$) and pH (7.6; 7.4) exhibited similar values at both locations. There were, however, considerable differencs in water temperature (discussed later) between the regulated and unregulated streams.

Experimental procedures — Alder (*Alnus tenuifolia*) leaves were collected in September 1978 immediately prior to abscission. The leaves were air-dried then oven-dried at 60°C for 48 h and weighed into 5-g units and strung on monofilament line. A single leaf pack was lashed to each brick and placed into a riffle area of each stream on September 29. After 48 h, three replicate leaf packs were retrieved from each site to serve as leaching controls. Thereafter five replicates were collected from each site after 17, 38, 52, and 66 d in the stream. At the time of collection the leaf pack was cut free of the brick and placed into a plastic bag containing 5% formalin. In the laboratory the leaf pack was thoroughly rinsed with tap water to remove accumulated sediments, dried at 60°C for 48 h, and weighed (±0.1 g). Macroinvertebrates associated with the leaf pack were placed into 80% EtOH until identified and enumerated. Dry weight of macroinvertebrates was determined following drying to constant weight at 60°C. No attempt was made to correct for weight loss during preservation. Water temperatures were monitored using maximum–minimum thermometers at each site.

Results — There were clear difference in leaf processing rates (Fig. 1A). On each sampling date leaf packs from the Colorado River had less weight remaining than those from the Fraser River. Analysis of variance showed these differences to be significant ($P <$

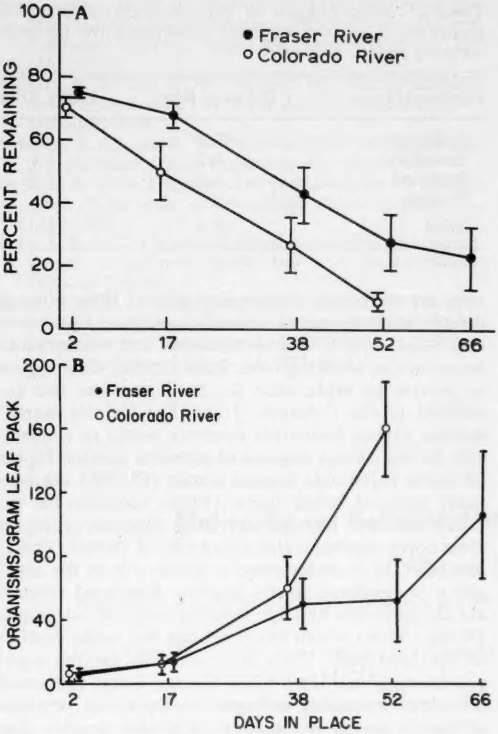

FIG. 1. A) Decomposition of alder leaf packs in the Fraser River and Colorado River, Colorado, September 29 through December 3, 1978. Mean value ± 1 SD; B) Colonization of leaf packs by macroinvertebrates plotted as organisms per dry weight of leaf pack remaining. Mean value ± 1 SD.

0.05) on each sampling date except day 38 ($0.05 < P < 0.10$). Even losses due to leaching exhibited significant differences between sites. Gelroth and Marzolf (1978) found that leaf packs apparently lost weight by leaching to a greater degree in a natural stream than a channelized stream. These results are difficult to reconcile since leaching is thought to be a purely physical process unrelated to variables such as temperature (Petersen and Cummins 1974).

Leaf packs collected from the Colorado River site were >90% processed after 52 d in the stream (Fig. 1A). Thus leaf packs were not again collected at this site. The Fraser River samples collected on January 7 (day 100) consisted only of monofilament line as either the leaf packs had been completely processed or were damaged by ice action. The leaf packs collected on this date were therefore not included in the analysis.

After accounting for leaching losses, linear regression was used to estimate the loss rate coefficient (k) following $\log_e$ transformation of the percent remaining data in Fig. 1A. This assumes that leaf pack processing in streams follows an exponential decay model (Petersen and Cummins 1974). These estimates are presented below along with calculated times for 50 and 90% processing.

Site	k	50%	90%
Colorado River	0.0462	15	50
Fraser River	0.0235	30	98

The k values for both sites indicate rapid processing of alder leaf packs with the Colorado River loss rate coefficient approximately twice that of the Fraser River. Leaves with k values above 0.010 are considered "fast" species (Petersen and Cummins 1974). Alder leaf packs would be 90% processed in just 50 d at the Colorado River site, a rate of processing nearly equal to that obtained by Hart and Howmiller (1975) for *Alnus rhombifolia* leaves in a much warmer southern California stream.

Although numbers of macroinvertebrates per leaf pack were generally similar at the two sites (Fig. 1B), there were obvious differences in the species composition (Table 1). Eight of the taxa collected in the Fraser River leaf packs were not found in the Colorado River samples. Six taxa were collected only from the Colorado River. These differences undoubtedly relate to the effects of stream regulation (Ward and Short 1978). The most abundant species collected at both sites was the mayfly *Ephemerella infrequens* which accounted for 76% of the total number of macroinvertebrates in the Colorado River leaf packs and 34% in the Fraser River samples. Many taxa in the Colorado River leaf packs were present in very low numbers (Table 1); often only 1 or 2 individuals were collected during the entire study period (e.g. *Tricorythodes* sp., *Skwala parallela, Pteronarcella badia, Lepidostoma* sp.). This occurred to a much lesser degree in the Fraser River leaf packs.

Assignment of the macroinvertebrates to functional groups (Merritt and Cummins 1978) also reveals drastic differences between the sites (Table 2). Collectors were by far the dominant group in the Colorado River leaf packs, mainly due to the presence of large numbers of *Ephemerella infrequens.* Shredders were much less important at the location below Granby Dam. In the Fraser River leaf packs, the collectors formed the bulk of the biomass, but the shredder biomass value was 10× that found in the Colorado River samples. Alder leaves incubated in a small headwater stream in Colorado (Short et al. 1980) had an even greater shredder biomass than the Fraser River samples, yet the loss rate coefficient ($k = 0.0308$) was less than that of the Colorado River below Granby Dam where shredders were virtually absent.

Minimum and maximum water temperatures recorded at intervals over the sampling period are shown below.

Time interval	Colorado River	Fraser River
Oct. 1–Oct. 15	9.4–13.3	1.1–13.1
Oct. 15–Nov. 5	7.2–13.1	0–9.4
Nov. 5–Nov. 19	5.0–10.0	0–5.6
Nov. 19–Dec. 3	4.6–7.8	0
Dec. 3–Jan. 7	1.7–5.3	0

The effect of impoundment was to elevate fall and winter temperatures and to increase thermal constancy (see Ward 1976b).

Discussion — The results of this study do not support our hypothesis that reduction of shredders would result in a slower processing of leaf litter in the regulated stream.

Temperature appears to be one factor to which the differences in leaf processing rates between the streams may be attributed. Weight loss of leaf litter often is directly proportional to stream temperature (Anderson and Sedell 1979). The elevated fall and winter water temperatures resulting from Lake Granby thus appear to provide an explanation for the higher loss rate coefficient in the Colorado River. The "winter warm" thermal regime below the reservoir seems to compensate for the virtual absence of shredder species. Inputs of coarse particulate organic matter (CPOM) are normally reduced below dams (which accounts for reduced shredder populations) since instream transport from upper reaches is eliminated (Ward 1976a). Therefore, CPOM probably plays a minor role in the energetics of regulated stream reaches. Regulated streams are characterized by large standing crops of autotrophs (Ward 1976a) which likely provide the major portion of the food base. What then accounts for the rapid processing of leaf litter below Granby Dam? Enhanced microbial processing at higher temperatures provides at least a partial explanation. It is also possible that surficial scraping by the large numbers of *E. infrequens* significantly contributed to weight loss of Colorado River leaf packs. Elevated temperature may increase leaf weight loss by increasing feeding activities of macroinvertebrates.

TABLE 1. Mean numbers of macroinvertebrates per leaf pack over the entire sampling period. Functional group classification based on Merritt and Cummins (1978): S = shredder, C = collector, G = grazer, and P = predator. + denotes <0.1.

Taxon	Colorado River	Fraser River	Functional group
Ephemeroptera			
Baetis sp.	2.6	6.2	C
Ephemerella grandis	+	1.0	C
Ephemerella infrequens	38.2	26.4	C
Paraleptophlebia sp.	0.5	5.7	C
Rhithrogena sp.	0	1.1	C/G
Tricorythodes sp.	+	0	C
Plecoptera			
Alloperla sp.	0	5.0	P
Skwala parallela	+	0	P
Cultus sp.	0	0.8	P
Claassenia sabulosa	0	+	P
Pteronarcys californica	0	+	S
Pteronarcella badia	0.1	0.1	S
Capnia sp.	0	0.5	S
Trichoptera			
Arctopsyche sp.	0	2.0	C
Hydropsyche sp.	+	2.5	C
Brachycentrus sp.	0.2	0.2	C
Glossosoma sp.	+	0.8	C/G
Lepidostoma sp.	0.1	22.4	S
Rhyacophila angelita	+	0	P
Diptera			
Chironomidae	4.5	2.2	C/G
Simulium sp.	2.1	0.3	C
Atherix pachypus	0.6	0	P
Coleoptera			
Optioservus sp.	0	0.7	C/G
Gastropoda			
Physa sp.	+	0	G
Turbellaria			
Polycelis coronata	1.1	0	P
Total	50.0	77.9	

TABLE 2. Mean biomass of macroinvertebrate functional groups (mg/g leaf pack) collected in leaf packs over the entire sampling period. + denotes <0.1.

Functional group	Colorado River	Fraser River
Collectors	40.9	10.3
Shredders	0.2	2.0
Predators	1.4	2.0
Grazers	+	+
Total	42.5	14.3

It is not known whether the findings of the present study are applicable to regulated streams in other regions or even to other lotic systems in the Rocky Mountains. The proliferation of dams necessitates a fuller understanding of the effects of stream regulation and provides a setting for testing and developing basic theories of stream ecology.

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A Motion for the Retirement of the Von Bertalanffy Function

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ROFF, D. A. 1980. A motion for the retirement of the von Bertalanffy function. Can. J. Fish. Aquat. Sci. 37: 127–129.

The reasons for the continued use of the von Bertalanffy equation are examined. It is suggested that these reasons are insufficient to overcome the drawbacks of this function and alternative procedures are recommended.

Key words: von Bertalanffy, growth, yield per recruit

ROFF, D. A. 1980. A motion for the retirement of the von Bertalanffy function. Can. J. Fish. Aquat. Sci. 37: 127–129.

Nous analysons les raisons pour lesquelles on continue d'utiliser l'équation de von Bertalanffy. Nous suggérons que ces raisons sont insuffisantes pour l'emporter sur les désavantages de cette fonction, et nous recommandons d'autres méthodes.

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ONE of the most ubiquitous equations in the fisheries literature is the von Bertalanffy function. Historically it gained wide currency because it claimed to be developed from bioenergetic principles. However, as pointed out by several authors (Parker and Larkin 1959; Paloheimo and Dickie 1964; Ursin 1967) this equation, from a bioenergetic perspective, is at best a special case and at worst nonsense (Knight 1968). Given that the equation can no longer be justified on the grounds upon which it was developed, why has it remained so much in use? In this note I examine the reasons for this and suggest that they do not outweigh the disadvantages of the von Bertalanffy equation.

Probably the most general reason for the continued use of this equation is that it is a convenient statistical description of the data. But is it so convenient? There are principally two statistical reasons for selecting a particular equation: firstly, the equation may be very flexible and fit a wide range of data and secondly the equation may be easily fitted to the data. The first is certainly true of the von Bertalanffy function but the second is decidely not true, as testified by the recurrence of papers providing methods of fitting it and other

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logistic type curves (Walford 1946; Yoshihara 1950; Tomlinson and Abramson 1961; Fabens 1965; Grosenbaugh 1965; Allen 1966; Bhattacharya 1966; Ricklefs 1967; Rafail 1973; R. K. Misra unpublished data). Indeed, if one was given the task of designing an equation that was extremely difficult to fit in a statistically satisfactory manner the von Bertalanffy function is precisely the sort one might come up with! Its particular form defies transformation to some statistically tractable model and all methods call for iterative solutions which make statistical testing difficult. Although, as previously stated, the von Bertalanffy function is flexible with respect to its shape it always assumes that an asymptotic length exists, which, when there is no evidence of curvature in the data leads to some ridiculous fits (Knight 1968). From a statistical point of view, what we require is a function that is flexible in shape, reduces to a linear function, and can be fitted to data using some standard technique such as least-squares estimation. Knight (1969) suggested that in some circumstances a parabola might be a reasonable model. Rafail (1972) suggested a modified parabola as an alternative model and showed that in several fish species, plaice, haddock, North Sea cod, North Sea sole, and *Serranus alandrinnus*, this parabola gives as good a fit or better than the von Bertalanffy equation. Rafail's modification makes the fitting of this equation rather tedious. However, the normal form of the parabola, $L_t = a + bt + ct^2$, where L_t is length at time t and a, b, c are constants (which can be fitted by the standard least-squares method) is quite sufficient. This may be demonstrated by considering how well a parabola can be fitted to data generated under the most restrictive assumption that fish are actually growing according to the von Bertalanffy function.

The number of ages observed in a population varies with k and L_∞ (Beverton and Holt 1959). This variation must be taken into consideration when comparing the parabolic fit to the von Bertalanffy equation. Using the data of Beverton and Holt (1959) to define the set of most frequently observed combinations of L_∞, k, and number of ages I compared the difference in predicted sizes between the von Bertalanffy function and a parabola fitted to this equation by the method of least squares. This measure is defined as $\frac{1}{n}\sum_{t=1}^{n}\left|\frac{V_t - P_t}{P_t}\right| \times 100\%$, where V_t is the predicted size given by the von Bertalanffy function, P_t that from the parabola and n the number of age-groups. The largest mean percentage difference between the two functions is only approximately 5% and for over 90% of the combinations the difference is less than 3%. This difference would have been even smaller if the first 1 to 6 age-groups (the number depending on the particuar combination of L_∞ and k) had been ignored as is done in most studies because these age-groups are not caught. Thus, *even if the fish grew according to the von Bertalanffy function* the fit obtained with the parabola would be, in most cases, indistinguishable from that obtained with the von Bertalanffy equation. It would seem that the parabola will fit a wider range of data than even Knight (1968) gives it credit for! The great advantage of the parabola is that it may be fitted by standard statistical techniques which are available in "canned" statistical computer programes. Further, multiple growth curves can be compared statistically and the equation reduces to a linear function and hence there is no attempt to force asymptotic behavior when none is observed.

It should not be thought that I am advocating the replacement of the von Bertalanffy function with the parabola. The choice of a particular equation should be dictated by circumstances: for example, if t_0 is very small the growth curve may be linearized, in some cases, by taking logarithms of the variables (this procedure may also stabilize the variances which is desirable for linear regression analysis). The analysis of the growth of witch (*Glyptocephalus cynoglossus*) by Bowers (1960) clearly demonstrates the usefulness of this approach.

Another reason for remaining faithful to the von Bertalanffy function is that it is used in the Beverton–Holt yield per recruit model. In the days of abaci and slide rules an easily obtained solution of this model for an arbitary growth function was not available and hence the solutions given by Beverton (1954) and Jones (1957), presuming a von Bertalanffy growth equation, were of considerable value. But these are the days of the digital computer and there are a host of "canned" routines available to integrate the yield function numerically. There is, therefore, absolutely no reason to be tied to any particular growth function.

The final reason for continuing to use the von Bertalanffy function is that it permits a comparison of growth curves already found in the literature. However, the variety of techniques used to fit this equation and the differences in their errors make comparisons, albeit non-statistical, highly suspect. However, if comparisons are desired there is no reason why the von Bertalanffy equation should not be fitted to the data for this purpose but another model used for other purposes, although for the reasons given I do not favor this practise with respect to equations that do not permit statistical comparison.

Whether the von Bertalanffy growth equation was an intellectual breakthrough or a statistical blunder is a subject for historians of science; but it has most assuredly outworn its usefulness and I put forward the motion for its retirement.

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PERSPECTIVES

The River Continuum Concept[1]

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From headwaters to mouth, the physical variables within a river system present a continuous gradient of physical conditions. This gradient should elicit a series of responses within the constituent populations resulting in a continuum of biotic adjustments and consistent patterns of loading, transport, utilization, and storage of organic matter along the length of a river. Based on the energy equilibrium theory of fluvial geomorphologists, we hypothesize that the structural and functional characteristics of stream communities are adapted to conform to the most probable position or mean state of the physical system. We reason that producer and consumer communities characteristic of a given river reach become established in harmony with the dynamic physical conditions of the channel. In natural stream systems, biological communities can be characterized as forming a temporal continuum of synchronized species replacements. This continuous replacement functions to distribute the utilization of energy inputs over time. Thus, the biological system moves towards a balance between a tendency for efficient use of energy inputs through resource partitioning (food, substrate, etc.) and an opposing tendency for a uniform rate of energy processing throughout the year. We theorize that biological communities developed in natural streams assume processing strategies involving minimum energy loss. Downstream communities are fashioned to capitalize on upstream processing inefficiencies. Both the upstream inefficiency (leakage) and the downstream adjustments seem predictable. We propose that this River Continuum Concept provides a framework for integrating predictable and observable biological features of lotic systems. Implications of the concept in the areas of structure, function, and stability of riverine ecosystems are discussed.

Key words: river continuum; stream ecosystems; ecosystem structure, function; resource partitioning; ecosystem stability; community succession; river zonation; stream geomorphology

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De la tête des eaux à l'embouchure, un réseau fluvial offre un gradient continu de conditions physiques. Ce gradient devrait susciter, chez les populations habitant dans le réseau, une série de réponses aboutissant à un continuum d'ajustements biotiques et à des schémas uniformes de charge, transport, utilisation et emmagasinage de la matière organique sur tout le

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parcours d'une rivière. Faisant appel à la théorie de l'équilibre énergétique des spécialistes de la géomorphologie fluviale, nous avançons l'hypothèse que les caractéristiques structurales et fonctionnelles des communautés fluviatiles sont adaptées de façon à se conformer à la position ou condition moyenne la plus probable du système physique. Nous croyons que les communautés de producteurs et de consommateurs caractéristiques d'un segment donné de la rivière se mettent en harmonie avec les conditions physiques dynamiques du chenal. Dans des réseaux fluviaux naturels, on peut dire que les communautés biologiques forment un continuum temporel de remplacements synchronisés d'espèces. Grâce à ce remplacement continu, il y a répartition dans le temps de l'utilisation des apports énergétiques. Ainsi, le système biologique vise à un équilibre entre une tendance vers l'utilisation efficace des apports d'énergie en partageant les ressources (nourriture, substrat, etc.), d'une part, et une tendance opposée vers un taux uniforme de transformation de l'énergie durant l'année, d'autre part. A notre avis, les communautés biologiques habitant dans des cours d'eau naturels adoptent des stratégies de transformation comportant une perte minimale d'énergie. Les communautés d'aval sont organisées de façon à tirer profit de l'inefficacité de transformation des communautés d'amont. On semble pouvoir prédire à la fois l'inefficacité (fuite) d'amont et les ajustements d'aval. Nous suggérons ce concept d'un continuum fluvial comme cadre dans lequel intégrer les caractères biologiques prévisibles et observables des systèmes lotiques. Nous analysons les implications du concept quant à la structure, fonction et stabilité des écosystèmes fluviaux.

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Statement of the Concept

Many communities can be thought of as continua consisting of mosaics of integrading population aggregates (McIntosh 1967; Mills 1969). Such a conceptualization is particularly appropriate to streams. Several workers have visualized streams as possessing assemblages of species which respond by their occurrences and relative abundances to the physical gradients present (Shelford 1911; Thompson and Hunt 1930; Ricker 1934; Ide 1935; Burton and Odum 1945; Van Deusen 1954; Huet 1954, 1959; Slack 1955; Minshall 1968; Ziemer 1973; Swanston et al. 1977; Platts 1979). Expansion of this idea to include functional relationships has allowed development of a framework, the "River Continuum Concept," describing the structure and function of communities along a river system. Basically, the concept proposes that understanding of the biological strategies and dynamics of river systems requires consideration of the gradient of physical factors formed by the drainage network. Thus energy input, and organic matter transport, storage, and use by macroinvertebrate functional feeding groups may be regulated largely by fluvial geomorphic processes. The patterns of organic matter use may be analogous to those of physical energy expenditure proposed by geomorphologists (Leopold and Maddock 1953; Leopold and Langbein 1962; Langbein and Leopold 1966; Curry 1972). Further, the physical structure coupled with the hydrologic cycle form a templet (Southwood 1977) for biological responses and result in consistent patterns of community structure and function and organic matter loading, transport, utilization, and storage along the length of a river.

Derivation of the Concept

As the cyclic theory for explaining the evolution of land forms and streams (young, mature, ancient) proved unsatisfactory, the concepts gradually were replaced by a principle of dynamic equilibrium (Curry 1972). The concept of the physical stream network system and the distribution of watersheds as open systems in dynamic ("quasi") equilibrium was first proposed by Leopold and Maddock (1953) to describe consistent patterns, or adjustments, in the relationships of stream width, depth, velocity, and sediment load. These "steady state" systems are only rarely characterized by exact equilibria and generally the river and its channel tend toward a mean form, definable only in terms of statistical means and extremes (Chorley 1962); hence, the idea of a "dynamic" equilibrium. The equilibrium concept was later expanded to include at least nine physical variables and was progressively developed in terms of energy inputs, efficiency in utilization, and rate of entropy gain (Leopold and Langbein 1962; Leopold et al. 1964; Langbein and Leopold 1966). In this view, equilibration of river morphology and hydraulics is achieved by adjustments between the tendency of the river to maximize the efficiency of energy utilization and the opposing tendency toward a uniform rate of energy use.

Based upon these geomorphological considerations, Vannote initially formulated the hypothesis that structural and functional characteristics of stream communities distributed along river gradients are selected to conform to the most probable position or mean state of the physical system. From our collective experience with a number of streams, we felt it was possible to translate the energy equilibrium theory from the physical system of geomorphologists into a biological analog. In this analysis, producer and consumer communities characteristic of a given reach of the river continuum conform to the manner in which the river system utilizes its kinetic energy in achieving a dynamic equilibrium. Therefore, over extended river reaches, biological communities should become established which approach equilibrium with the dynamic physical conditions of the channel.

Implications of the Concept

It is only possible at present to trace the broad outlines of the ways the concept should apply to stream ecosystems and to illustrate these with a few examples for which reasonably good information is available. From headwaters to downstream extent, the physical variables within a stream system present a continuous gradient of conditions including width, depth, velocity, flow volume, temperature, and entropy gain. In developing a biological analog to the physical system, we hypothesize that the biological organization in rivers conforms structurally and functionally to kinetic energy dissipation patterns of the physical system. Biotic communities rapidly adjust to any changes in the redistribution of use of kinetic energy by the physcial system.

STREAM SIZE AND ECOSYSTEM STRUCTURE AND FUNCTION

Based on considerations of stream size, we propose some broad characteristics of lotic communities which can be roughly grouped into headwaters (orders 1–3), medium-sized streams (4–6), and large rivers (>6) (Fig. 1). Many headwater streams are influenced strongly by the riparian vegetation which reduces autotrophic production by shading and contributes large amounts of allochthonous detritus. As stream size increases, the reduced importance of terrestrial organic input coincides with enhanced significance of autochthonous primary production and organic transport from upstream. This transition from headwaters, dependent on terrestrial inputs, to medium-sized rivers, relying on algal or rooted vascular plant production, is thought to be generally reflected by a change in the ratio of gross primary productivity to community respiration (P/R) (Fig. 2). The zone through which the stream shifts from heterotrophic to autotrophic is primarily dependent upon the degree of shading (Minshall 1978). In deciduous forests and some coniferous forests, the transition probably is approximately at order 3 (Fig. 1). At higher elevations and latitudes, and in xeric regions where riparian vegetation is restricted, the transition to autotrophy may be in order 1. Deeply incised streams, even with sparse riparian vegetation, may be heterotrophic due to side slope ("canyon") shading.

Large rivers receive quantities of fine particulate organic matter from upstream processing of dead leaves and woody debris. The effect of riparian vegetation is insignificant, but primary production may often be limited by depth and turbidity. Such light attenuated systems would be characterized by $P/R < 1$. Streams of lower order entering midsized or larger rivers (e.g. the 3rd order system shown entering the 6th order river in Fig. 1) have localized effects of varying magnitude depending upon the volume and nature of the inputs.

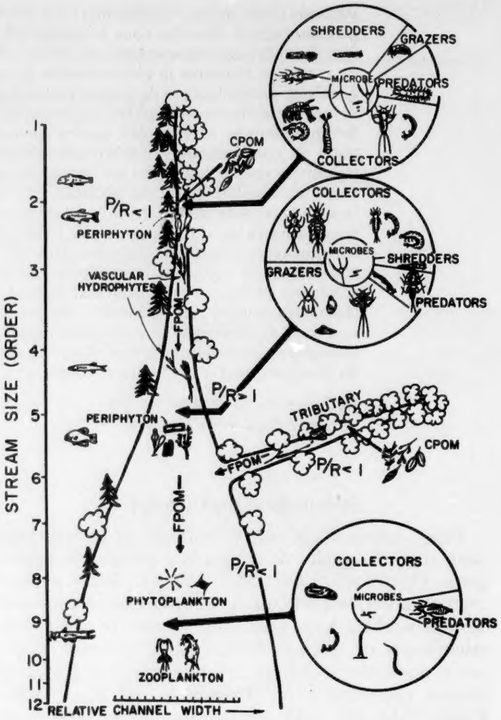

FIG. 1. A proposed relationship between stream size and the progressive shift in structural and functional attributes of lotic communities. See text for fuller explanation.

The morphological–behavioral adaptations of running water invertebrates reflect shifts in types and locations of food resources with stream size (Fig. 1). The relative dominance (as biomass) of the general functional groups — shredders, collectors, scrapers (grazers), and predators are depicted in Fig. 1. Shredders utilize coarse particulate organic matter (CPOM, >1 mm), such as leaf litter, with a significant dependence on the associated microbial biomass. Collectors filter from transport, or gather from the sediments, fine and ultrafine particulate organic matter (FPOM, 50 μm–1 mm; UPOM 0.5–50 μm). Like shredders, collectors depend on the microbial biomass associated with the particles (primarily on the surface) and products of microbial metabolism for their nutrition. Scrapers are adapted primarily for shearing attached algae from surfaces. The proposed dominance of scrapers follows shifts in primary production, being maximized in midsized rivers

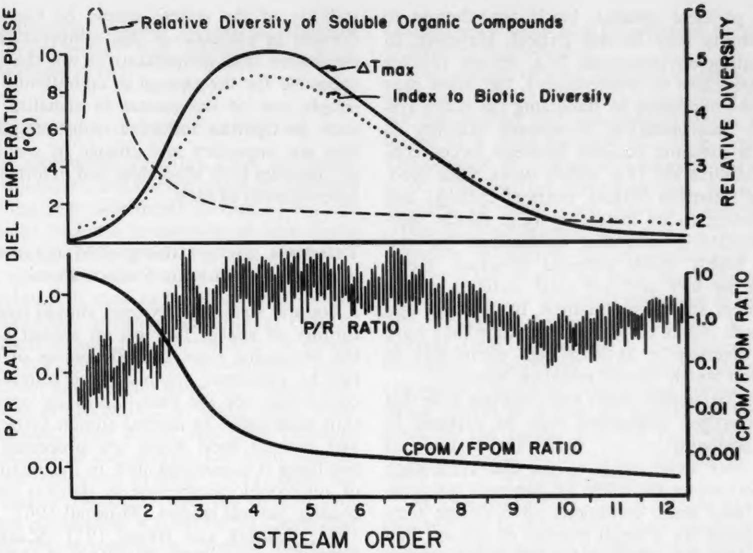

Fig. 2. Hypothetical distribution of selected parameters through the river continuum from headwater seeps to a twelfth order river. Parameters include heterogeneity of soluble organic matter, maximum diel temperature pulse, total biotic diversity within the river channel, coarse to fine particulate organic matter ratio, and the gross photosynthesis/respiration ratio.

with $P/R > 1$. Shredders are hypothesized to be codominant with collectors in the headwaters, reflecting the importance of riparian zone CPOM and FPOM–UPOM derived from it. With increasing stream size and a general reduction in detrital particle size, collectors should increase in importance and dominate the macroinvertebrate assemblages of large rivers (Fig. 1).

The predatory invertebrate component changes little in relative dominance with stream order. Fish populations (Fig. 1) show a shift from cool water species low in diversity to more diverse warm water communities (e.g. Huet 1954). Most headwater species are largely invertivores. Piscivorous and invertivorous species characterize the midsized rivers and in large rivers some planktivorous species are found — reflecting the semi-lentic nature of such waters.

The expected diversity of soluble organic compounds through the continuum is shown in Fig. 2 (dashed line). Headwater streams represent the maximum interface with the landscape and therefore are predominantly accumulators, processors, and transporters of materials from the terrestrial system. Among these inputs are heterogeneous assemblages of labile and refractory dissolved compounds, comprised of short- and long-chain organics. Heterotrophic use and physical absorption of labile organic compounds is rapid, leaving the more refractory and relatively high molecular weight compounds for export downstream. The relative importance of large particle detritus to energy flow in the system is expected to follow a curve similar to that of the diversity of soluble organic compounds; however, its importance may extend further downstream.

Thus the river system, from headwaters to mouth, can be considered as a gradient of conditions from a strongly heterotrophic headwater regime to a seasonal, and in many cases, an annual regime of autotrophy in midreaches, and then a gradual return to heterotrophic processes in downstream waters (Fisher 1977). Major bioenergetic influences along the stream continuum are local inputs (allochthonous litter and light) and transport from upstream reaches and tributaries (Fig. 1). As a consequence of physical and biological processes, the particle size of organic material in transport should become progressively smaller down the continuum (reflected by CPOM:FPOM ratio in Fig. 2, except for localized input of lower order tributaries) and the stream community response reflect progressively more efficient processing of smaller particles.

River Ecosystem Stability

Stability of the river ecosystem may be viewed as a tendency for reduced fluctuations in energy flow, while community structure and function are maintained, in the face of environmental variations. This implicitly couples community stability (sensu Ricklefs 1979) to the instability ("noise") of the physical system. In highly stable physical systems, biotic contribution to ecosystem stability may be less critical. However, in widely fluctuating environments (e.g. stream reaches with lage fluctuations in temperature), the biota may assume critical importance in stabilizing the entire system. In this interpretation, ecosystem stability is achieved by a dynamic balance between forces contributing to stabilization (e.g. debris dams, filter feeders, and other retention devices; nutrient cycling) and those contributing to its instability (e.g. floods, temperature fluctuations, microbial epidemics). In systems with a highly stable physical structure, biotic diversity may be low and yet total stability of the stream ecosystem still be maintained. In contrast, systems with a high degree of physical variation may have high species diversity or at least high complexity in species function which acts to maintain stability.

For example, in stream zones experiencing wide diel temperature changes, organisms may be exposed to suboptimum temperatures for significant portions of the day, but over some range in the diel cycle each organism encounters a favorable or optimum temperature range. Under these conditions an optimum temperature will occur for a larger number of species than if the thermal regime displayed minimum variance. Also, in the thermally fluctuating system, many populations have an opportunity to process energy, and as temperatures oscillate around a mean position, various populations may increase or decrease their processing rates. Thus, an important aspect of the predictably fluctuating physical system is that it encompasses optimum conditions for a large number of species. This interplay between physical and biological components can be seen in terms of ecosystem stability by considering the response of total biotic diversity in the river channel as balanced against the maximum diel temperature range (ΔT max) (Fig. 2). Headwater streams in proximity to groundwater supply or infiltration source areas exhibit little variation in ΔT max. With increased distance from subsurface sources and separation of the forest canopy, ΔT max will attain its widest variance because of increased solar input. The ΔT max amplitude is greatly diminished in high order streams due to the buffering effect of the large volume of water in the channel (Ross 1963). In headwater springs and brooks, diversity may be low because biological communities are assembled from those species which can function within a narrow temperature range on a restricted nutritional base; the stability of the system may be maintained by the low amplitude of diel and annual temperature regimes. Total community diversity is greatest in medium-sized (3rd to 5th order in Fig. 2) streams where temperature variations tend to be maximized. The tendency to stabilize energy flow in midsized streams may be aided by high biotic diversity which mitigates the influence of high variance in the physical system as characterized by ΔT max; i.e. variation due to fluctuating thermal regimes should be offset by a high diversity of biota. In large rivers, stability of the system should be correlated with reduction in variance of diel temperature. We wish to emphasize that temperature is not the only factor responsible for the change in community structure; it is simply one of the easiest to visualize. Other factors such as riparian influence, substrate, flow, and food also are important and change in predictable fashion downstream both absolutely and in terms of the relative heterogeneity of each.

TEMPORAL ADJUSTMENTS IN MAINTAINING AN EQUILIBRIUM OF ENERGY FLOW

Natural stream ecosystems should tend towards uniformity of energy flow on an annual basis. Although the processing rates and efficiencies of energy utilization by consumer organisms are believed to approach equilibrium for the year, the major organic substrates shift seasonally. In natural stream systems, both living and detrital food bases are processed continuously, but there is a seasonal shift in the relative importance of autotrophic production vs. detritus loading and processing. Several studies (Minshall 1967; Coffman et al. 1971; Kaushik and Hynes 1971; MacKay and Kalff 1973; Cummins 1974; Sedell et al. 1974) have shown the importance of detritus in supporting autumn-winter food chains and providing a fine particle base for consumer organisms during other seasons of the year. Autotrophic communities often form the major food base, especially in spring and summer months (Minshall 1978).

Studies on headwater (order 1–3) streams have shown that biological communities in most habitats can be characterized as forming a temporal sequence of synchronized species replacement. As a species completes its growth in a particular microhabitat, it is replaced by other species performing essentially the same function, differing principally by the season of growth (Minshall 1968; Sweeney and Vannote 1978; Vannote 1978; Vannote and Sweeney 1979). It is this continuous species replacement that functions to distribute the utilization of energy inputs over time (e.g. Wallace et al. 1977). Individuals within a species will tend to exploit their environment as efficiently as possible. This results in the biological system (composite species assemblage) tending to maximize energy consumption. Because some species persist through time and because new species become dominant, and these too are exploiting their environment as efficiently as possible, processing of energy by the changing biological system tends to result in uniform energy processing over time. Thus, the biological system moves towards equilibrium by a trade-off between a tendency to make most efficient use of energy inputs through resource partitioning of food, substrate, temperature, etc. and tendency toward a uniform rate of energy processing throughout the year. From strategies observed on small to medium-sized streams (orders 1–5), we propose that biological communities, developed in natural streams in dynamic equilibrium, assume processing strategies involving minimum energy loss (termed maximum "spiraling" by Webster 1975).

ECOSYSTEM PROCESSING ALONG THE CONTINUUM

The dynamic equilibrium resulting from maximization of energy utilization and minimization of variation in its use over the year determines storage or leakage of energy. Storage includes production of new tissue and physical retention of organic material for future processing. In stream ecosystems, unused or partially processed materials will tend to be transported downstream. This energy loss, however, is the energy income, together with local inputs, for communities in downstream reaches. We postulate that downstream communities are structured to capitalize on these inefficiencies of upstream processing. In every reach some material is processed, some stored, and some released. The amount released in this fashion has been used in calculating system efficiency (Fisher 1977). Both the upstream inefficiency (leakage) and the downstream adjustments seem predictable. Communities distributed along the river are structured to process materials (specific detrital sizes, algae, and vascular hydrophytes) thereby minimizing the variance in system structure and function. For example, materials prone to washout, such as flocculant fine-particle detritus, might be most efficiently processed either in transport or after deposition in downstream areas. The resistivity of fine particle detritus to periodic washout is increased by sedimentation in depositional zones or by combination in a matrix with the more cohesive silt and clay sediments. Thus, enhanced retention results in the formation of a distinct community adapted to utilize this material. The minimization of the variance of energy flow is the outcome of seasonal variations of energy input rates (detritus and autotrophic production), coupled with adjustments in species diversity, specialization for food processing, temporal expression of functional groups, and the erosional–depositional transport and storage characteristics of flowing waters.

TIME INVARIANCE AND THE ABSENCE OF SUCCESSION IN STREAM COMMUNITIES

A corollary to the continuum hypothesis, also arising from the geomorphological literature (Langbein and Leopold 1966), is that studies of biological systems established in a dynamically balanced physical setting can be viewed in a time independent fashion. In the context of viewing adaptive strategies and processes as continua along a river system, temporal change becomes the slow process of evolutionary drift (physical and genetic). Incorporation of new functional components into the community over evolutionary time necessitates an efficiency adjustment towards reduced leakage. In natural river systems, community structure gains and loses species in response to low probability cataclysmic events and in response to slow processes of channel development.

The concept of time invariance allows integration of community structure and function along the river without the illusion that successional stages are being observed at a given location in a time-dependent series. The concept of biological succession (Margalef 1960) is of little use for river continua, because the communities in each reach have a continuous heritage rather than an isolated temporal composition within a sequence of discrete successional stages. In fact, the biological subsystems for each reach are in equilibrium with the physical system at that point in the continuum. The concept of heritage implies that in natural river systems total absence of a population is rare, and biological subsystems are simply shifting spatially (visualize a series of overlapping normal species-abundance curves in which all species are present at any point on the spatial axis but their abundance differs from one point to the next) and not in the temporal sense typical of plant succession.

On an evolutionary time scale, the spatial shift has two vectors: a donwstream one involving most of the aquatic insects and an upstream one involving molluscs and crustaceans. The insects are believed to have evolved terrestrially and to be secondarily aquatic. Since the maximum terrestrial–aquatic interface occurs in the headwaters, it is likely that the transition from land to water first occurred here with the aquatic forms then moving progressively downstream. The molluscs and crayfish are thought to have developed in a marine environment and to have moved through estuaries into rivers and thence upstream. The convergence of the two vectors may explain why maximum species diversity occurs in the midreaches.

Conclusion

We propose that the River Continuum Concept provides a framework for integrating predictable and observable biological features of flowing water systems with the physical–geomorphic environment. The model has been developed specifically in reference to natural, unperturbed stream ecosystems as they operate in the context of evolutionary and population time scales. However, the concept should accommodate many unnatural disturbances as well, particularly those which alter the relative degree of autotrophy:heterotrophy (e.g. nutrient enrichment, organic pollution, alteration of riparian vegetation through grazing, clear-cutting, etc.) or affect the quality and quantity of transport (e.g. impoundment, high sediment load). In many cases, these alterations can be thought of as reset mechanisms which cause the overall continuum response to be shifted toward the headwaters or seaward depending on the type of perturbation and its location on the river system.

A concept of dynamic equilibrium for biological communities, despite some difficulties in absolute definition, is useful because it suggests that community structure and function adjust to changes in certain geomorphic, physical, and biotic variables such as stream flow, channel morphology, detritus loading, size of particulate organic material, characteristics of autotrophic production, and thermal responses. In developing a theory of biological strategies along the river continuum, it also should be possible to observe a number of patterns that describe various processing rates, growth strategies, metabolic strategies, and community structures and functions. Collection of extensive data sets over the long profile of rivers are needed to further test and refine these ideas.

Acknowledgments

The ideas presented here have been refined through discussions with our associates in the River Continuum Project, especially T. L. Bott, J. D. Hall, R. C. Petersen, and F. J. Swanson; and other colleagues including S. A. Fisher, C. A. S. Hall, L. B. Leopold, F. J. Triska, and J. B. Webster. We are grateful to J. T. Brock, A. B. Hale, C. P. Hawkins, J. L. Meyers, and J. R. Moeller for their constructive criticism of a draft version of the manuscript. This work was supported by the U.S. National Science Foundation, Ecosystems Studies program under grant numbers BMS-75-07333 and DEB-7811671.

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BOOK REVIEWS/COMPTES RENDUS

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Food Webs and Niche Spaces. *Joel E. Cohen. Monographs in Population Biology, No. 11. Princeton University Press, Princeton, NJ. 1978. xv + 189 p. $14.00 (paper $6.95).*

The thesis of this monograph is that "a niche space of dimension one suffices, unexpectedly often and perhaps always, to describe the trophic niche overlaps implied by real food webs in single habitats." Using the combinatorial theory of interval graphs, Cohen analyzes data from 31 published food webs — a majority of which are aquatic in some sense — and finds that most of them (more than would be expected under any of several null hypotheses) are "interval," which means that it is possible for their trophic niche overlaps to be described in one dimension. This is not the same as saying that they *are* one-dimensional. For example, points arranged along an L-shaped line can be displayed in one dimension even though the L-shape requires two dimensions. However, if a niche overlap graph were *not* interval, then the trophic structure could not be one-dimensional.

Despite problems with assumptions and definitions, the results are not trivial — for example: (1) a one-dimensional model is apparently adequate as a "most parsimonious" trophic niche model; (2) the poor fit of some of MacArthur's models to field data can be blamed on failure of assumptions other than their being one-dimensional models; (3) source food webs (one or more kinds of organisms plus all that directly or indirectly depend on them for food), in contrast to community and sink food webs, are inadequate for analysis of trophic structure; (4) the ratio of the number of kinds of prey in a community to the number of kinds of predators approximates a constant ¾, and (5) a model of trophic structure in which "every kind of predator has a constant and independant probability of preying on every kind of prey, with a probability that is characteristic of the food web" appears to be an adequate model. This book is also valuable as an example of a new methodology for analysis of biological communities, including: (1) the use of graph theory; (2) use of the computing system APL for model building, data analysis and data simulation; (3) the simulation of data under various null hypothesis models, including an example of the danger of assuming that "random number generators" are generating random numbers, and (4) pointing out that detection of correlated niche dimensions (say food particle size and some quality of the food positively correlated with food particle size) as separate dimensions is impossible.

It is difficult to explain or make use of some of the results, but Cohen is aware of this and takes great pains to consider the consequences of the model, the assumptions, ambiguities in definitions, and the implications if the conclusions are correct. He does so excessively in some places, taking up much space with the examination of various points from all possible angles. The result is certainly a monograph. In a short paper, Cohen (1977. Proc. Natl. Acad. Sci. 74: 4533–4536.) says in 3½ pages most of what this book says in 131 pages (not counting the appendices which contain the source data — the food web matrices — and any lengthy derivations). An example of the style at its worst (p. 100–102): "These models also supplement the assumption of a one-dimensional niche space with other assumptions. The details of these other assumptions strongly influence the predictions of the models. Consequently, the conclusions of these models follow from one-dimensionality in conjunction with other assumptions, but not from one-dimensionality per se." First person plural is used frequently, producing the "royal We" effect after a while.

In general the treatment is rigorous, but Cohen is not immune to slippery logic. On p. 44 he refuses to dismiss a model (one which turns out to be supported by the data) that is admitted to be biologically unrealistic, but on p. 102 he dismisses one of MacArthur's models because it is biologically unrealistic — even though it predicts correctly under at least some circumstances. On p. 6 and subsequently, the hypotheses and analyses are explicitly limited to the trophic dimensions of niche space, but on p. 103 a discrepancy between results and prediction is explained by possible overlaps along unobserved nontrophic dimensions.

I am worried most by the ambiguity of some of the definitions on which biological interpretations of the analysis results depend (as it worries Cohen — see discussion beginning p. 118). For example, "habitat" is first defined on p. 21 in a very casual way — as being uniform with respect to something thought to be important. The central thesis of the book pertains to "real food webs in single habitats" and the importance of knowing whether the data are from a single habitat or a composite of habitats is emphasized, as on pp. 98 and 104. Yet at several points (e.g. p. 40) Cohen refers to the difficulty of distinguishing between single and composite habitats, and to the imprecision of the definition, while at the same time using the distinction to interpret results. "Kind" of organism is another vaguely defined term. Introduction of the word "subniches" into an argument (p. 102) without discussion of what subniches are and how they relate to niches, is reminiscent of museum taxonomists coping with a vague species concept by resorting to subspecies. Niche "overlap" is defined in an unambiguous (though nonquantitative) way (p. 6), at least operationally; however, since it is concluded that high overlap is not equivalent to high competition but only implies the possibility of high competition, I fail to see the relevance of the critique of "competition" on p. 24–26 to the analysis of food webs which follows. MacArthur's definition, that "two species are competing if an increase in either one harms the other," is rejected on the grounds that "the definition makes it impossible to say that two species are competing without a natural or artificial perturbation experiment." My impression is that most ecologists think it *is* impossible, given any meaningful definition of competition.

This is an important contribution and aquatic biologists — including fisheries biologists — should at least be aware of its conclusions and their implications. It is idea-stimulating rather than definitive, but that is not a criticism. I found myself pondering possible applications of canonical variate analyses and multidimensional scaling analysis to the testing of similar hypotheses with quantitative trophic attribute data, and that is surely the kind of response Cohen wished to provoke.

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Coral Reefs: Research Methods. *Edited by D. R. Stoddart and R. E. Johannes. UNESCO. Monographs on oceanographic methodology, Vol. 5. 1978. xv + 581 p.*

Coral Reefs: Research Methods was conceived by a Scientific Committee on Oceanic Research (SCOR) Working Group, set up in 1971 to consider standardization of techniques used in coral reef studies. It is the second attempt to bring together methodologies for the study of reefs. Whereas the first monograph, a *Handbook for Atoll Research*, published 26 years ago, covered geography, meteorology, hydrology, soils, botany, zoology, marine ecology, and anthropology of atolls, the present volume focuses upon the marine ecology of the coral reefs themselves.

The book covers methods for defining the physical structure of reef ecosystems (10 papers), techniques for quantifying the abundance and distribution of marine organisms (17 papers), and procedures for the measurement of energy and nutrient fluxes (16 papers). It is heavily weighted toward research development in the U.S., Australia, and the U.K. (90% of contributions are from these three countries, with over 50% from the U.S.). Australian and U.K. input is limited to the sections on reef morphology and biotic distributions, whereas the U.S. emphasis is more pronounced in the chapter on energy and nutrient fluxes.

Contributions are limited to techniques specific for coral reefs, or where more general methodologies are included (i.e. surveying, aerial photography, productivity), the problems and modifications unique to coral reefs are discussed. Generally, standard methods developed for other ecosystems, but easily translated to the reef environment, are excluded. For this we must commend the editors.

The first chapter deals with defining the external and internal physical structure of reefs. Techniques of surveying and mapping (Stoddart) are complimented by close-range aerial balloon photography (Rützler) and long-range aerial and satellite photography (Hopley). Hopley's paper also includes a wealth of information on the technical problems and advantages of various imagery and remote sensing techniques. Simple drills for obtaining cores from reef environments are described by Thom (land-based) and by Macintyre (underwater). Stoddart outlines the mechanical analysis of reef sediments. Although radiometric dating of reefs is apparently fraught with a number of technical and theoretical difficulties, Chappell et al. give an excellent discussion of the state of the art and include a set of useful procedures to be followed when attempting to date reefs in this way. Stoddart discusses the problems with present reef terminology, and proposes some criteria for standardizing it.

The second chapter deals with the distribution and abundance of reef organisms. Five papers deal with various aspects of measuring coral colonies: quadrat methods are covered by Pichon, Scheer, and Kinzie and Snider; plotless and transect methods are given excellent treatment by Loya, and the application of phytosociological methods to coral distribution is demonstrated by Scheer. Visual surveys are often used to monitor changes over large areas of reef, but suffer from subjectivity. Kenchington addresses the problems of observer precision and discusses useful techniques for visual observation.

A series of five papers follows, with practical techniques for the measurement of noncolonial cryptofauna (Hutchings), soft-bottom communities (Thomassin), sponges (Rützler), nemertina (Kirsteuer), and reef fishes (Russel et al.). Although many other important groups inhabiting coral reefs have been excluded (for example, coral-burrowing molluscs and polychaetes), this selection of papers describes techniques which are applicable to most of them. To this chapter on biotic distributions should be added four papers from the third chapter which deal with measurement of phytoplankton (Holm-Hansen), zooplankton using drift nets (Johannes), zooplankton using diver-pushed nets (Porter et al.), and bacteria (Wiebe). As a step toward data handling, Peake et al. outline a data storage/retrieval system which has proved useful for the Royal Society of London's reef research on Aldabra.

The last chapter of the book, entitled Energy and Nutrient Flux, covers four general topics: productivity (gross primary productivity and respiration), growth (whole reef calcification, and coral ecology growth), nutrient measurement, and coral feeding. Several papers which deal more with biotic distribution have already been mentioned.

Four excellent papers deal with productivity. Marsh and Smith present O_2 and CO_2 techniques for measuring productivity and respiration in water flowing across reefs. McCloskey et al. discuss the interpretation of photosynthesis and respiration in individual corals, and the relationship of the ecological P/R ratio to the physiology of polyp-zooanthellae symbiosis. Kinsey shows how productivity can be measured in still-water environments induced by low tides or artificial field enclosures. Smith and Kinsey extend these techniques to the laboratory. As background to all flowing water techniques, Maragos outlines simple methods for measuring water volume transport across reefs.

Growth is examined as calcification on a whole reef scale by Smith (flowing water), Kinsey (still water), and by Kinsey and Smith (laboratory studies). Other measures of individual coral colony growth involve use of dyes (Lamberts), buoyant weight techniques (Jokiel et al.), and coral sectioning (Buddemeier). Porter outlines a useful technique for examining the gut contents of coral polyps.

Finally, nutrient measurement in the coral reef environment requires modifications to standard methods. Modifications are suggested for TOC (Gordon), POC (Marshall), nitrogen (Webb), and phosphorus (Pilson). D'Elia outlines a general protocol for the determination of N, P, and organic C.

In summary, the book is essential reading for anyone conducting ecological studies in a coral reef ecosystem. It should not be taken as the final word on technique, however, for many of the papers present only first-attempt solutions to the unique problems of the coral reef. Nevertheless, the book does fulfill its purpose, which is to contribute toward the standardization of technique and comparability of measurement when coral reef data are collected.

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Books received/Livres reçus[1]

August/Aout 1979

***Sampling Design and Statistical Methods for Environmental Biologists.** *Roger H. Green. John Wiley & Sons, Inc., Somerset, NJ. 1979. xi + 257 p. $19.95.* (A much needed book on certain specialized aspects of statistics, especially aimed at what this Editor would call "impact assessment ecology.")

***Predator–Prey Systems in Fisheries Management.** *Edited by Henry Clepper. Sports Fishing Institute, Washington, D.C. 1979. viii + 504 p. $20.00 (in U.S.); $23.00 (elsewhere).* (Compiled from the International Symposium on Predator–Prey Systems in Fish Communities and their Role in Fisheries Management, held at Atlanta, Georgia, July 24–27, 1978.)

***Reservoirs. Brian Henderson-Sellers.** *MacMillan Press Ltd., London and Basingstoke, U. K. 1979. x + 128 p. £3.95.* (A small, soft-cover book, multidisciplinary in approach, but kept as nontechnical as possible.)

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[1] Entries in this list *not* marked by an asterisk are available for review by interested readers for a 3-month period from the time of publication of the list. For information, please write to the Book Review editor.

[1] Les ouvrages inclus dans cette liste et *non* accompagnés d'un astérisque peuvent être mis à la disposition de lecteurs intéressés qui voudraient en faire l'analyse, et ce, pour une période de 3 mois à compter de la date de parution de la liste. Pour plus de renseignements, veuillez écrire au rédacteur des Comptes rendus.

ANNOUNCEMENTS/AVIS

International Association for Great Lakes Research (IAGLR)

The annual conference, Great Lakes — 80, of the International Association for Great Lakes Research (IAGLR) will be held May 19–22, 1980 at Queen's University, Kingston, Ontario. In addition to scientific sessions, the conference theme "Towards An Ecosystem Management Strategy" will be addressed by a number of internationally known scientists and environmental managers. Contributed papers on the conference theme and on any aspect of science relevant to the Great Lakes are welcomed. Further information can be obtained from Dr E. D. Ongley, Conference Chairman, Great Lakes — 80, Queen's University, Kingston, Ontario K7L 3N6, (613) 547–5781.

Association internationale de recherche sur les Grands Lacs (IAGLR)

La conférence annuelle, Les Grands Lacs — 80, de l'Association internationale de recherche sur les Grands Lacs (IAGLR) se tiendra du 19 au 22 mai 1980 à l'Université Queen's, à Kingston, en Ontario. En plus de séances scientifiques, le thème de la conférence « Vers une stratégie de gestion des écosystèmes » fera l'objet de présentations par plusieurs scientifiques et gestionnaires de l'environnement de réputation internationale. Les contributions sur le thème de la conférence et sur tout aspect de la science touchant les Grands Lacs sont les bienvenues. Pour plus de renseignements, on est prié de s'adresser au Dr E. D. Ongley, président de la conférence, Les Grands Lacs — 80, Université Queen's, Kingston, Ontario K7L 3N6, (613) 547–5781.

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

Influences of anadromous spawning behavior and optimal environmental conditions upon striped bass (*Morone saxatilis*) year-class strength **R. E. Ulanowicz and T. T. Polgar**

Optimal assay conditions for serum and liver glutamate oxaloacetate transaminase, glutamate pyruvate transaminase, and sorbitol dehydrogenase from the rainbow trout, *Salmo gairdneri* **S. d'Apollonia and P. D. Anderson**

Oxygen transport in salmon spawning gravels **R. A. Johnson**

Effect of individual variability on the von Bertalanffy growth equation **K. J. Sainsbury**

Effects of dietary ascorbic acid on chronic lead toxicity to young rainbow trout (*Salmo gairdneri*) **P. V. Hodson, J. W. Hilton, B. R. Blunt, and S. J. Slinger**

Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan **J. Janssen and S. B. Brandt**

Factors controlling oxygen depletion in ice-covered lakes **J. A. Mathias and J. Barica**

Distribution of fatty acids in lipids of the common Atlantic sea urchin *Strongylocentrotus droebachiensis* **T. Takagi, C. A. Eaton, and R. G. Ackman**

Growth of underyearling sockeye salmon (*Oncorhynchus nerka*) under constant and cyclic temperatures in relation to live zooplankton ration size **R. M. Biette and G. H. Geen**

Role of a unionid clam population in the calcium budget of a small Arctic lake **R. H. Green**

Correlation and prediction of metal toxicity to aquatic biota **K. L. E. Kaiser**

Mortality, hematocrit, osmolality, electrolyte regulation, and fat depletion of young-of-the-year freshwater fishes under simulated winter conditions **M. L. Toneys and D. W. Coble**

Harvesting strategies and parameter estimation for an age-structured model **R. B. Deriso**

Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations **M. C. Healey**

Influence of secondarily treated kraft mill effluent on the accumulation rate of attached algae in experimental continuous-flow troughs **M. L. Bothwell and J. G. Stockner**

Effects on rainbow trout (*Salmo gairdneri*) of a chronic exposure to waterborne selenium **P. V. Hodson, D. J. Spry, and B. R. Blunt**

Notes

Confidence intervals for optimal effort estimates from the Schaefer production model **R. L. McGaw**

Chromosome complement of the marine worm *Neanthes arenaceodentata* (Polychaeta: Annelida) **G. G. Pesch and C. E. Pesch**

Sex determination of the ommastrephid squid *Illex illecebrosus* using beak morphometrics **M. C. Mercer, R. K. Misra, and G. V. Hurley**

Techniques for exploring and presenting data applied to lake phosphorus concentration **K. H. Reckhow**

Letters/Lettres: Comment on estimated escapement of Atlantic salmon (*Salmo salar*) for maximum smolt production in rivers of different productivity **A. S. Gee**; Reply **P. E. K. Symons**. Comment on optimal survey design **R. H. Green**; Reply **W. Cuff**

Canadian
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Sciences

Guide for Authors

CONTENT

We welcome manuscripts reporting significant new information in the broad fields of fisheries management and technology, ocean science, and aquatic environments relevant to Canada. Manuscripts must not have been submitted or accepted for primary publication elsewhere. In general, manuscripts reporting fragments of research are unacceptable, as are those of mainly local interest.

Articles: Studies of broad scope that are original contributions to science.

Notes: Differ from articles on the basis of scope or completeness, rather than quality of research. They may report significant new knowledge arising from problems with narrow, readily defined limits, or important findings that warrant immediate publication before broader studies are complete. Notes should occupy no more than 3 printed (9 manuscript) pages.

Reviews: Detailed critical appraisals of broad areas of investigation, particularly those that have developed rapidly in recent years.

Perspectives: Essays of opinion or hypothesis on aquatic science that are of concern to the professional and layman. References are desirable; informal style is welcomed

Letters and Comments: Opinion on topics recently discussed in the *Journal*; preferred maximum length, 500 words.

EDITORIAL PRACTICES

The *CBE Style Manual* (4th ed. AIBS, Arlington, Va. 22209) is used as the authority in matters of form. The standards for spelling are *Webster's Third New International Dictionary* and *le Grand Larousse Encyclopédique*. Titles of periodicals are abbreviated as in the *Bibliographic Guide for Editors & Authors* list. References to literature are made by the name-and-year system. The *Journal* follows the names and spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (3rd ed. 1970) Spec. Publ. No. 6, American Fisheries Society. All measurements must be metric and SI units are preferred.

Series titles should be avoided. An *abstract* is required for all manuscripts, and should state concisely, in less than 250 words, what was done, found, and concluded. Up to 10 *key words* should follow the abstract.

Each manuscript is normally submitted to two *referees.* Contributors are encouraged to suggest names of potential referees.

Illustrations should be submitted in triplicate as photographic reproductions. They should not be mounted, stapled, or clipped. Symbols, letters, and numerals must be neat, and at least 1.5 mm high when the illustration is reduced to column width. Drawings should, when possible, be grouped to facilitate comparisons.

Proofs are sent to the author, who is responsible for correcting errors in typesetting. *Alterations to the content must be avoided.*

Fifty *reprints* are supplied free. Additional reprints may be purchased at the time of publication (an order form is sent with the proofs). A charge of $44.00 per page is made for articles published. When submitting a manuscript, an author should state that his institution will accept this charge.

CHECKLIST ON MANUSCRIPTS

Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed, and organized to facilitate comparisons? Are there inconsistencies between tables or figures and the text, or within the text? Should some of the data be made available separately, in a data or manuscript report or at a data repository? If you use statistical analysis are the statistics subordinate to the research?

Would any of the text be clearer if condensed? Are summary statements given at the beginning of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the *title* encompass the content of the report? Does the *abstract* give the essentials of the new knowledge? Is the *introduction* largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem? Are details of *materials and methods* limited to what scientists need in understanding the design of the study and in judging adequacy of the data? Are generalizations on the *results* adequate? Are findings distinguished from inferences from them? Is *discussion* limited to interpretation and significance of the findings?

Journal
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halieutiques
et aquatiques

Guide des Auteurs

SUJET

Les manuscrits comportant une information nouvelle et significative dans le vaste domaine de la gestion et de la technologie des pêches, des sciences de la mer et des milieux aquatiques au Canada sont les bienvenus. Ils ne devront pas avoir été soumis ou acceptés pour publications dans d'autres périodiques de fonds. En général, les manuscrits portant sur des fragments de recherche sont inacceptables, car ils n'ont qu'un intérêt local.

Articles: Études d'une portée générale, constituant des contributions inédites à la science.

Notes: Se distinguent des articles par la portée et le degré d'achèvement plutôt que par la qualité des recherches. Elles peuvent signaler une connaissance nouvelle et significative découlant de problèmes étroitement limités et facilement définis, ou d'importantes découvertes qui méritent d'être publiées avant que des études plus vastes ne soient terminées. Les notes ne doivent pas dépasser 3 pages imprimées (9 pages de manuscrit).

Critiques: Appréciations critiques détaillées de vastes champs de recherches, particulièrement dans les domaines ayant connu de rapides progrès au cours des dernières années.

Perspectives: Essais portant sur une opinion ou une hypothèse relative aux sciences aquatiques qui intéressent professionnels et profanes. Il est préférable de donner des références et d'écrire, si possible, dans un style simple.

Lettres et commentaires: Opinions sur des sujets récemment exposés dans le *Journal*. Longueur maximale préférable: 500 mots.

DISPOSITION GÉNÉRALES

Le *CBE Style Manual* (4e éd. AIBS, Arlington, Va. 22209) sert de guide quant à la forme de la présentation. Le *Webster's Third New International Dictionary* et le *Grand Larousse Encyclopédique* font autorité pour l'orthographe des mots. Les titres de périodiques sont abrégés suivant le *Bibliographic Guide for Editors & Authors*. Les références bibliographiques dans le texte doivent suivre le système nom de l'auteur-année. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenus dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (3e éd. 1970) Publ. spéc. no 6, American Fisheries Society. Toutes les mesures doivent être conformes au système métrique, de préférence en unités SI.

On devra éviter les *articles en séries*. Un *résumé* doit accompagner chaque texte et doit exposer brièvement, en moins de 250 mots, ce qui a été fait, ce qui a été découvert et les conclusions auxquelles on est arrivé. Le résumé doit être suivi d'un nombre de *mots clés* ne dépassant pas 10.

Chaque texte est soumis d'ordinaire à deux *arbitres*. Nous encourageons les collaborateurs à suggérer les noms d'arbitres possibles.

Les *illustrations* doivent être soumises en triple sous forme de reproductions photographiques. Elles ne doivent pas être montées, brochées ni coupées. Les symboles, lettres ou chiffres doivent se détacher avec précision lorsque l'illustration est réduite à la largeur de la colonne. Les dessins doivent, autant que possible, être groupés pour faciliter l'étude comparative.

L'auteur doit revoir les *épreuves* qu'on lui remet et en corriger les erreurs typographiques. *Il doit éviter de changer le contenu du texte.*

Cinquante *tirés à part* sont fournis gratuitement. Des tirés à part supplémentaires peuvent être achetés au moment de la publication. (Un bon de commande à cet effet accompagne les épreuves.) Les frais sont de $44.00 par page pour la publication d'articles. Quand un auteur soumet un manuscrit, il doit préciser que son institution accepte les frais.

LISTE DE CONTRÔLE POUR MANUSCRITS

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les éditeurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes au but de l'étude?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou dans le texte même? Est-ce que certaines données devraient être présentées séparément, dans un rapport manuscrit ou dans un dépôt de données? Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la recherche?

Le texte y gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction?

Le *titre* est-il représentatif du contenu du rapport? Le *résumé* donne-t-il l'essentiel des connaissances nouvelles? L'*introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème? La section *matériel et méthode* contientelle le minimum de détails qui permettront aux autres scientifiques de saisir les grandes lignes de l'étude et de juger de la valeur des données? Les généralisations sur les *résultats* sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions? La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes?

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Guide for Typists Preparing Copy

Read "Guide for Authors". When in doubt about how to type or arrange details, follow *Journal* practice.

Type the manuscript on white bond paper, not flimsy, preferably 21.5 × 28 cm (8.5 × 11 inches). If possible, use paper with the lines numbered in the margin. Leave all margins at least 2.5 cm wide.

Double-space all parts of the manuscript, including tables, captions for illustrations, footnotes, and the reference list. Underline only material that is to be printed in italics. Indent the first line of each paragraph in the text and of each footnote.

In titles and headings, capitalize the first letter of each word. For small capitals, use small letters.

Indicate all text footnotes by superscript arabic numerals. Number them consecutively throughout the manuscript, starting with those on the title page. Place each footnote immediately below the reference to it, separating it from the text by horizontal lines.

Type the title, the author's names and affiliations, related footnotes, the running head, the abstract with its bibliographic citation, and key words on the first page (see Appendix A). Number all pages beginning with the title page, including those for tables and captions for illustrations.

Have the author check the finished manuscript, and send the ribbon copy and two other clear copies to the Scientific Information and Publications Branch.

A detailed guide with appendices is available from the Scientific Information and Publications Branch.

Abbreviations: Abbreviations used frequently in the *Journal* are listed in Appendix B.

Tables: Examine the current volume of the *Journal* to see how tables are set up (see Appendix C).

Note especially the following concerning *numbered tables:*

Type each on a separate page, using paper without the lines numbered.

Number them with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed with the text, and seldom need horizontal lines (see Appendix C).

Illustrations: Send three photographic reproductions (no larger than 21.5 × 28 cm) of each illustration with the manuscript. Type the author's name and figure number on a strip of paper and fasten it to the back of the print. Do not write or type on the illustration itself. Also, type the captions in succession on a separate page.

Where each figure is first referred to, type in the margin "Fig. — near here."

Mathematical Expressions, Equations, and Formulas: Leave three spaces above and below lines that have much material in superscripts, and above and below equations and formulas. In the various expressions, place each component in its correct position (see Appendix D).

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter *l* and the numeral *one*, and between the capital *O* and the numeral *zero*. Make other explanatory notes similarly.

References: Check the text to see that all references in the list are referred to. Type the reference list, double-spaced, in the style used in the *Journal* (see Appendix E). Type names of journals in full or abbreviate according to the *Bibliographic Guide for Editors & Authors*.

Headings: If the levels of importance of your heads and subheads are not apparent from their positions, identify each of them with an appropriate circled number or letter in the left-hand margin of the typed page: 1 or A for the highest level, 2 or B for the second level, 3 or C for the third level. Or include with your manuscript a typed list of heads and subheads, indented as necessary to indicate their relative importance.

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Guide pour les secrétaires d'auteurs

Lisez le « Guide des auteurs ». Si vous avez des doutes sur la façon de dactylographier le texte ou d'en agencer les détails, suivez la pratique du *Journal*.

Dactylographiez le manuscrit sur papier blanc de bonne qualité, et non sur papier pelure, mesurant de préférence 21.5 × 28 cm (8.5 × 11 pouces). Si possible, employez un papier avec lignes numérotées en marge. Laissez toujours une marge d'au moins. 2.5 cm.

Tout le manuscrit, y compris tableaux, légendes de figures, renvois et références bibliographiques, devra être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique. Mettez en retrait la première ligne de chaque paragraphe du texte et de chaque renvoi.

Dans les titres et les en-têtes, n'employez la majuscule que pour la première lettre de chaque mot. Pour les petites majuscules, employez les minuscules du dactylographe.

Indiquez tous les renvois du texte par des chiffres arabes suscrits. Numérotez les renvois consécutivement par tout le texte, à commencer par ceux de la page titre. Placez chaque renvoi directement sous sa référence, le séparant du texte par des lignes horizontales.

Sur la première page, dactylographiez le titre, les noms et affiliations des auteurs, les renvois qui s'y rapportent, le titre courant, le résumé avec sa référence bibliographique et les mots clés (voir annexe A). Numérotez toutes les pages, à commencer par la page-titre, de même que celles contenant les tableaux et les légendes des illustrations.

Voyez à ce que l'auteur vérifie le manuscrit final, et soumettez la première copie ainsi que deux copies lisibles à la Direction de l'information et des publications scientifiques.

Un guide détaillé y compris des annexes est disponible gratis de la Direction de l'information et des publications scientifiques.

Abréviations: Nous donnons à l'annexe B une liste d'abréviations communément utilisées dans le *Journal*.

Tableaux: Consultez une copie du *Journal* pour la composition des tableaux (voir annexe C).

Portez une attention particulière à ce qui suit au sujet des *tableaux numérotés*:

Dactylographiez chaque tableau sur feuille séparée, vous servant de papier sans lignes numérotées.

Numérotez les tableaux en chiffres arabes.

Tracez des lignes horizontales au-dessus et audessous des entêtes et au-dessous des colonnes, rarement ailleurs. Ne tracez jamais de lignes verticales; laissez plutôt des espaces supplémentaires.

Indiquez les renvois dans les tableaux par les minuscules suscrites et placez les renvois au bas du tableau.

Placez les tableaux à la suite des références bibliographiques.

À l'endroit où le tableau est mentionné pour la première fois, indiquez dans la marge « Tableau — près d'ici ».

Remarquez que les *tableaux dans le texte* ne sont pas numérotés, sont dactylographiés avec le texte et ne requièrent que rarement des lignes horizontales (voir annexe C).

Illustrations: Envoyez avec le manuscrit trois reproductions photographiques (21.5 × 28 cm ou moins) pour chaque illustration. Dactylographiez le nom de l'auteur et le numéro de la figure sur une lisière de papier que vous collerez au dos. N'écrivez pas à la main ou à la machine sur la photographie même. De plus, dactylographiez les légendes, dans l'ordre, sur feuille séparée.

À l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge « Fig. — près d'ici ».

Equations, formules et expressions mathématiques: Laissez trois espaces au-dessus et au-dessous des lignes renfermant des chiffres ou des lettres suscrits et souscrits, ou encore au-dessus et au-dessous d'équations et de formules. Placez chaque composante des différentes expressions dans la position qui lui est propre (voir annexe D).

Indiquez clairement tous les symboles. Epelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la lettre *l* et le chiffre *un*, et entre la majuscule *O* et la chiffre *zéro*. Insérez de la même façon toute autre note explicative.

Références: Vérifiez le texte afin de vous assurer que toutes les références apparaissant dans la liste bibliographique sont bien mentionnées dans le texte. Dactylographiez à double interligne dans le style en usage dans le *Journal* (voir annexe E). Ecrivez les noms des périodiques au long ou les abrégez suivant le *Bibliographic Guide for Editors & Authors*.

En-têtes: Si la position de vos en-têtes et sous-en-têtes ne suffit pas à indiquer leurs niveaux d'importance, identifiez chacun d'eux par un chiffre ou une lettre encerclé à la marge gauche de la page dactylographiée: 1 ou A pour le niveau supérieur, 2 ou B pour le deuxième niveau, 3 ou C pour le troisième niveau. Ou encore, transmettez avec votre manuscrit une liste dactylographiée d'en-têtes et de sous-en-têtes rentrés de façon à indiquer leur importance relative.

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